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THE NOCTURNAL AMPHIBIAN FAUNA OF THE SOUTHERN LAKE MICHIGAN BEACH

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It has been known that the toad, *Bufo woodhousii fowleri* Hinckley, frequents the sandy beach of southern Lake Michigan after dark on mild or warm nights throughout summer and fall. This behavior has been believed to be related to the potential food sources of the strand line (Shelford 1913; Hubbs 1918). The presence of frogs, not previously noted at the beach, also seemed to be accounted for by food abundance, through analogy with the toad. This would be a reasonable supposition were it not for the fact that the locations assumed by toads and frogs on the beach are unrelated to the proximity (or even the absence) of the strand line. Preliminary studies in 1947 indicated that an average marked toad could be expected on the beach once in five days, which makes the feeding explanation more questionable, since beach specimens always have full stomachs.

A series of observations was planned to clarify the relation of this nocturnal behavior to the needs of these amphibians. Other data were also collected (particularly for toads) on territoriality, density of populations, plumpness (*i.e.*, the relative excess or deficiency of body water), and the relations of these to climatology and micro-habitat. Unfortunately frogs were neither sufficiently abundant nor regular enough in behavior to permit treatment as complete as that for the toad.

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FIELD METHODS

Field data were collected after dark by walking along the edge of the lake on the wet sand between two fixed points. The western point was a pier on the east side of Burns Ditch; five thousand feet to the east, a store operated by the Krautshrunk family served as the other terminus. The amphibian fauna of this strip appeared to be in no way different from that casually observed in previous years on various other strips of beach up to ten miles east and several miles west of the Ditch.

With the aid of a lamp, toads could be seen at a distance of forty feet. A stop watch was started when leaving either end point and stopped a few feet from each amphibian encountered; the exact spot was marked with a heel mark. Adult toads were immediately placed in the weighing container (an aluminum salt-shaker with a large screw cap), and weighed by means of a balance, by adding dry sand to a small heavy paper envelope. The envelope was held by a cradle which was balanced with the empty weighing container. The envelopes, sealed by folding and fastening with paper clips, and carrying pertinent identification data, were found to be accurate to a tenth of a gram. They were subsequently weighed on a laboratory balance. Each toad was measured (snout to end of urostyle) to the nearest millimeter. If "new," the toad was marked by the use of individually numbered metal fingerling tags (Raney

and Lachner 1947) and then released. It was later found (Stille 1950) that the tags were not permanent; they were lost by cutting through the lower jaw bone. It is unlikely that tags were lost during the first season for any particular tagged toad.

The stop watch time can readily be converted into distance to give the locus of each amphibian encountered. Loci were determined most accurately near the end points of the beach strip. Near the midpoint, errors at least as large as fifty feet are to be expected. This estimate was based on the walking time from a trail about five hundred feet from the eastern end point. Each afternoon or evening this walking time was recorded and on leaving the beach the discrepancy in locating the trail by the earlier walking time was noted. No errors greater than twenty feet occurred. Since such errors would tend to increase in direct proportion to the distance, errors as large as one hundred feet would be expected at the midpoint twenty-five hundred feet away. However, two fixed points were used in determining the amphibian loci, so this interior error would be halved, yielding the estimate of fifty feet. Other sources of error, such as shoreline variations, were not measured.

It thus appears that weight data are accurate to a tenth of a gram, length measurements generally to a millimeter. Errors in determining loci on the beach are variable; they may range from something over one hundred feet near the midpoint to a few inches near the end points. No errors in toad enumeration, temperature readings, timing events, identification, bookkeeping, and calculations were discovered. The toads could not be sexed without dissection, and this datum is accordingly omitted in the present study.

No evidence of harmful effects of jaw tags on toads is available. The weight of a fingerling tag is about 0.13 gm.; this corresponds to a weight of 1.1 per cent of the lightest toad, 0.2 per cent of the heaviest toad, and 0.4 per cent of the mean of all toads tagged. No corrections were made for the presence of a tag in weight data, since the additional weight is of the order of rounding errors. Comparison of the weight of tagged toads with that of untagged toads, either within the same night or throughout the period of study, revealed no differences. Feeding seems unmodified, at least in volume. Raney (1940) found no differences in stomach contents between tagged and untagged frogs. Tagging effects on mortality are also absent. We would expect smaller toads to be affected by jaw tags more often than larger toads. The tenability of this expectation can be tested by means of a chi square test on the hypothesis of no effects on mortality or survival among size groups. If the smaller tagged toads are recaptured significantly less frequently relative to the larger toads, the null hypothesis is contradicted. In Table I toads are classified according to their length when originally marked. The number of recaptures possible computed from the number of times the "home range" of each toad was revisited is summed

TABLE I. *Test of the hypothesis that there are no detrimental effects on toad survival from tags*

Toads are classified by length at initial encounter. The number of recaptures "possible" reasonably predicts the number of recaptures "observed."

Length (mm.)	Number of recaptures		
	Possible*	Expected	Observed
64–72	26	5.65	4
63	23	5.00	8
61–62	38	8.26	9
60	29	6.30	8
58–59	44	9.56	10
56–57	38	8.26	7
48–55	46	9.99	7
Total	244	53.02	53

Chi square = 5.644, P = 0.47, for six degrees of freedom.

* The number of recaptures possible takes into account the number of times the "home range" of each toad was visited in the same season on nights following initial capture and marking. The number of nights are counted, not the number of times per night or nights, since behavior is modified as a consequence of handling.

for each length class. These classes were then pooled so as to obtain expected numbers equal to or greater than five. The numbers of observed recaptures are not significantly different from expected recapture numbers. With no detrimental tag effects a Chi square this large or larger would be expected to occur in approximately half of similar trials on continued sampling. The hypothesis of no detrimental effects appears to be supported. As far as our observations go, we are without evidence for detrimental tag effects on toads. If still smaller toads had been tagged, tagging effects on survival might have become conspicuous.

The time of encounter of the first amphibian of the evening, which happened to be a toad in every case, varied seasonally. Since initial amphibian appearance is later in the evening during summer, with the later time of sunset, it seems more natural to compare the event of toad appearance to sunset time rather than standard time. This tends to remove seasonal differences and reduces summer-to-fall discrepancies as great as sixty-five minutes to less than twenty minutes in the time of initial amphibian appearance.

The effects of temperature differences are as yet unmeasured. Cooler evening temperatures seem to retard the appearance of amphibians. Possible further refinements in predicting the time of initial amphibian appearance are to had by deriving a time of apparent sunset when the sky is obscured to varying degrees by clouds. A twilight time arbitrarily established might provide an even more natural base for the timing of certain biological events.

It has been tacitly assumed that amphibian beach-frequenting behavior is related to light intensity. Since changes of humidity and temperature, as well as of light intensity, are correlated with sunset, it would not be readily possible to single out light intensity as the most important factor in initiating the movement to the beach. Light intensity is, however, the most conspicuous factor; and this is particularly evident as sunrise approaches. An hour or so before sunrise, amphibians leave the beach. At this time other changes (temperature, humidity, etc.) lag further behind changes in light intensity.

A total of 134 toads were marked during the seasons of 1948–49; tagged toads were subsequently recovered on 75 occasions (Table I, Fig. 1). Data on dates and time of field work are available from Figure 2 for those nights on which toads were present on the beach and weighed. (Weight data were not taken on the first night of observations included in this study.) The numbers of frogs and juvenile toads observed are given in Table II.

Territoriality

As is evident from Figure 1, marked toads were subsequently encountered rather close to the locus of their previous capture and release. In no case was a displacement greater than five hundred feet noted. The mean displacement was 26.7 $\pm$ 15.0 ft. to the west, which is not significantly different from a zero displacement—tagged toads, at least, are quite localized. Changes in loci of five hundred feet or more would be expected to occur among toads substantially less frequently than once in one hundred similar observations. If we arbitrarily partition the beach into ten five hundred foot segments for study purposes, we can be reasonably sure that only very rarely will a toad be encountered more than one full segment away from its usual territory.

Since inversions occur in the order in which toads are located along the water's edge on different nights (Fig. 1), errors in fixing loci are not wholly responsible for differences in the recorded loci of individual toads. It seems remarkable that the variation in toad loci should be so slight, since the toads undoubtedly spend daylight hours farther than (but potentially as close as) 200 to 700 ft. south of the beach. This is evident from the toad tracks in the open sand near the beach. The general course of these tracks is per-

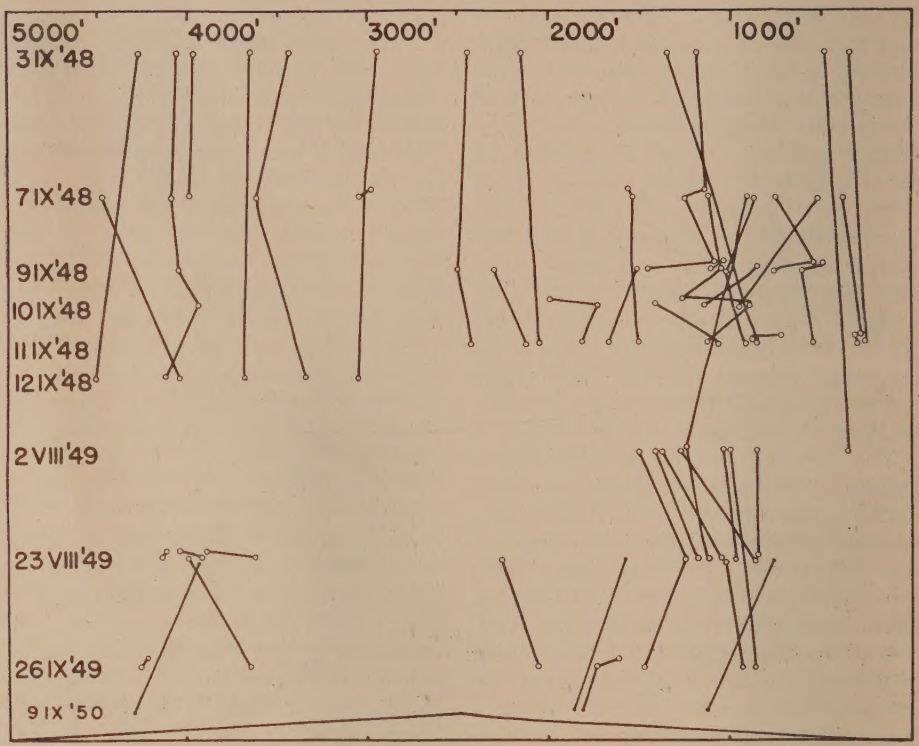

FIG. 1. Individual displacements of adult toads on different nights. The error expectation in determining a given locus, in excess of 50 ft. at 2,500 ft. from Burns Ditch, is indicated at the bottom of the figure.

pendicular to the beach; only rarely are toads found diurnally on the beach—three known specimens were juveniles and these were found under drift wood and debris.

Of particular interest are the six toads recaptured in the year following original marking (Fig. 1). Since toads have not been found on the beach early in the season, it is assumed that they are concentrated at the breeding ponds at this time. In summer, when the breeding season is over, the toads assume territories which are not greatly changed during the remainder of the year. Five of the six toads referred to above would have had to travel over a mile to and from the breeding ponds and their particular summer territories. If these five animals entered into breeding activities, we have much to learn on amphibian orientation; if these animals did not move to the distant breeding ponds, it would seem likely that a good segment of the local toad population is not included in the ancestry of later generations. Cursory surveys in adjacent areas have never revealed marked toads; hence it seems that beach loci, and presumably territories, of toads are stable from year to year.

Data for the bull frog, *Rana catesbeiana,* the green frog, *Rana clamitans,* and the leopard frog, *Rana pipiens,* are incomplete. Bull frogs and leopard frogs are likely to appear on successive nights, and it is presumed that all of the frogs are not merely transients. Like toads, the frogs leave tracks in the open sand, the course of the tracks being perpendicular to the beach.

Table II gives the frequency of different

TABLE II. *The numbers of different amphibian individuals seen on the beach*

On beach east of Burns Ditch	Adult *B. w. fowleri*	Juvenile *B. w. fowleri*	*Rana pipiens*	*Rana clamitans*	*Rana catesbeiana*
4–5,000 ft.	21	28	12	1	3
3–4,000 ft.	24	17	27	1	—
2–3,000 ft.	16	6	17	—	2
1–2,000 ft.	37	4	19	2	2
0–1,000 ft.	36	4	10	—	—
Total	134	59	85	4	7

Test of the similarity in distribution of the more abundant amphibians:

Comparison of distribution of adult *Bufo* and:	Degrees of freedom	Chi square	Significance level
Juvenile *Bufo*	4	35.050	.001
Rana pipiens	4	12.810	.02

amphibian individuals seen on the beach. Since no attempt was made to sample the various portions of the beach uniformly, comparisons are most readily made with the numerically superior toads. It appears that the leopard frogs and the juvenile toads are significantly different in distribution from the adult toads. (The beach frequencies of these frogs and small toads are included in Figure 3 with the same scale used to illustrate adult toad densities. The significance levels, indicated in the figure by maximum differences in the ordinates, are therefore not comparable to those of the adult toads.) Distribution differences will be discussed under "Environmental Relations."

TOAD DENSITY

The difference in loci, that is, the number of feet between two adult *Bufo,* is a function of the number of toads present at a given time on the beach. The average time of the encounter for each of two toads is readily obtained for each inter-*Bufo* distance. The mean of two distances gives the locus of the midpoint between them in feet from Burns Ditch. The means of these inter-*Bufo* distances, classified by time and beach segment containing the midpoint, are given in Table III.

For example, the first cell of Table III is empty since toads were rarely observed on the most easterly beach segment during the first 100 minutes after sunset, and so none of the midpoints of the distance between toads fell in this beach segment during this time interval. The next cell contains the number 204 which is the mean of those inter-*Bufo* distances whose midpoints fell within the most easterly beach segment during the second 100 minutes after sunset. Toad density along the beach is the reciprocal of the inter-*Bufo* distance; the mean of 204 ft. yields an estimate of average density of about 4.9 toads per 1000 feet. The means for beach segments and time intervals are the weighted means of all observations in the particular row or column. This procedure tends to bias the occurrence of large inter-*Bufo* distances away from arbitrarily chosen end segments and so reduces their means. Since the density differences, which seem so real in the field, are corroborated by the regularity in the observed inter-*Bufo* distances according to time and locus later found in the analysis

TABLE III. *The means of the inter-*Bufo *distances (in feet) by time and locus*

Loci to and including:	t in minutes after sunset			Means for beach segments
	$t \leqslant 100$	$100 < t \leqslant 200$	$200 < t$	
5,000 ft.	—	204	480	250
4,500 ft.	260	196	208	204
4,000 ft.	560	202	134	188
3,500 ft.	1310	284	500	541
3,000 ft.	—	1026	1440	1164
2,500 ft.	910	280	496	431
2,000 ft.	534	406	130	287
1,500 ft.	56	152	304	176
1,000 ft.	226	120	288	171
500 ft.	280	610	106	301
Means for time intervals	396	259	281	(286)

Complete analysis of variance*

Source	Degrees of freedom	Sum of squares	Mean square	F
Time intervals	2	253,880	126,940	1.23
Beach segments	9	32,644,320	3,627,148**	35.11
Interaction	16	3,931,052	244,280**	2.38
Individuals	155	—	403,320	—

* Data coded by division by ten.
** Denotes significance at the 1% level.

of the data, it would seem that this bias has not seriously distorted the information for the eastern arbitrarily determined end segment. (Toads rarely enter water; hence Burns Ditch provides a natural terminus on the other end of the beach studied.) From Figure 3 it is apparent that the average density of the eastern segment seems to be well within the range of expectations based on physiographic and physiological correlations to be discussed later.

The inter-*Bufo* distances, classified by time and location, were tested as to uniformity along the beach, uniformity through the night, and independence of time and place. Although the inter-*Bufo* distances were used in calculations, we shall discuss the results in terms of density. An analysis of variance (Table III) indicated significantly different densities along the beach and also the non-independence of time and place. Greater densities were found at certain places primarily during the first one hundred minutes after sunset. It turned out that those areas of greater and earlier density generally had in common vegetation available closer to the beach, steeper slopes to the water's edge, and a toad fauna lighter in weight. Hence, it seems reasonable that early or late toad appearance can be explained in terms of retarding effects. The appearance of toads is most retarded where individuals must travel greater distances over more nearly level terrain (not down steep slopes), and where the toads have excessive weight with respect to their length (Fig. 3).

Body Water Relations

It was found that individual toads usually gained weight when reweighed later on the same night. This increase in weight is suggestive of feeding while on the beach (Shelford 1913; Hubbs 1918; Hatt, VanTyne, Stuart, Pope and Grobman 1948) and on two occasions toads have been observed feeding on "washed in" monarch butterflies. However, gains as high as five grams and rates of gain of one-tenth of a gram per minute were observed in the field. The weights of the stomach contents of several toads of similar sizes were found to be inadequate for feeding to explain these gains, and, since small food animals were less abundant than toads on the wet sand of the beach, potential food sources are quite insufficient to account for the high rates of gain. (Toads have never been seen at the strand line, and when the strand line is present, tracks indicate that it is crossed without even pausing.)

Water is imbibed and urine production initiated as soon as frogs (*R. pipiens*) are placed in water (Adolph 1932). Increments of gain and rates of gain observed in toads in the field are readily duplicated in the laboratory by placing toads on moist substrata. It seems that water is imbibed by passive toads located on the wet sand strip of the beach, and feeding, if at all general, seems to be a minor consequence of beach visits.

Body water of amphibians may fluctuate widely without apparent ill effects. Hence, one of the major components of the weight of a toad is the relative abundance of body water in excess of the minimal quantity necessary for life. Another major component of toad weight is the mass of the non-aqueous parts of the animal along with minimal amounts of water necessary for life. This latter component is related, in general, to the cube of the length, and so may be estimated from length data. As noted above, beach toads always appear to have full stomachs. Presumably the weight of the stomach contents is also related to the cube of the length. By considering length and weight data together we may thus obtain some index of the relative amount of body water of field toads. A simple quotient of weight and length is ambiguous for it reflects a relative excess of body water as well as larger size.

In an effort to measure the relative excess or deficiency of body water the quotient of weight in grams by the cube of length in centimeters was computed for

each observation on a toad. This quotient will be termed "plumpness" for specimens with high plumpness values appear quite plump. Weight data are accurate to tenths of a gram and length data to millimeters; hence plumpness values have two significant figures. Where the same specimen was observed more than once on the same date the use of three figures is justified in considering changes during the night, for growth is not measurable and our interest is in variation in the numerator. Elsewhere the third figure in plumpness data is superfluous.

An analysis of plumpness data indicates a statistically significant tendency for toads of greater plumpness to be encountered later in the evening (Fig. 2). The plumpness increases of the few specimens reweighed twice on the same night reflect the general trend of the whole population studied. It thus seems reasonable to assume that this plumpness increase with time after sunset is due to water imbibition on the beach and is not solely a matter of the later arrival of specimens with larger plumpness values.

Dissimilarities in the means of water imbibition of frogs and toads are evident in the field in areas where the slope of the beach to the water's edge is not very great. Here the strip of wet sand is sometimes over forty feet wide. In such areas passive toads are usually found just within the wet sand boundaries while frogs apparently hop into the lake and are found at the water's edge. On nights when the lake is calm, areas may be found where the wet sand strip is about two feet wide and frogs and toads may be located within inches of each other.

Toads usually do not enter the water. The position eventually assumed by a toad of low plumpness on a wet substratum is such that the tarsus is farther away from the projection of the knee on the substrate, not under it as is the case if the substratum is dry. The effect of this position change is to put additional areas of the flanks or sides of the hind legs in contact

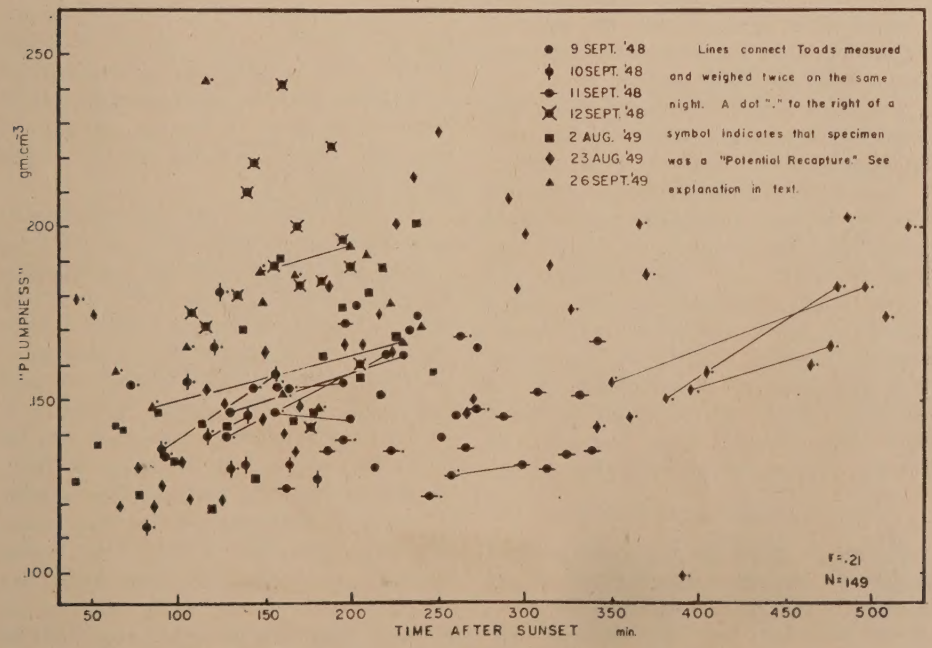

FIG. 2. Plumpness values of toads on different nights by minutes after sunset.

with the wet substrate. When visible, pulsations due to the posterior lymph hearts continue while a toad rests on a moist surface.

Toads encountered later in the evening are more likely to have been on the wet sand for varying lengths of time, possibly averaging over an hour, and are more likely to have urine (or water) in their bladders. Upon handling, these toads frequently void their urine. This rarely occurs in early evening when most toads have been on the beach much less than one half an hour. For this reason toads were immediately placed in the weighing container when encountered, after which voiding of the urine would not influence weight data.

The tracks indicate that only the feet of the toads touch the sand as they hop down the beach. Sensitivity of the feet to degrees of moisture may govern the halting of the animal before it reaches the lake. There are also differences in packing between wet and dry sand. Several trials seem to indicate that water intake is not lessened by reducing the area of the wet substratum in contact with the toad as long as the wrinkled groin area remains in contact with the water source.

Toads in regions removed from the Great Lakes have been observed frequenting the margins of rivers and ponds; hence it seems likely that nocturnal behavior resulting in water imbibition may be more general and include other amphibian populations than those of Lake Michigan. In several northern Illinois localities with a toad fauna, river and pond margins are apparently never visited. A high water table may account for an absence of this behavior. In a number of places where toads were obtained, water was available less than a foot below the surface.

Environmental Relations

Figure 3 gives an indication of the prominent terrain features south of the beach covered in this study. Sand removal operations ten years ago, by bulldozing to loading apparatus at railway stubs, filled in any ponds and marshes that may have occurred in this area. As mentioned earlier, this would mean that the amphibians studied have traveled distances up to well over a mile by any route. At most of the other localities along the lake potential breeding ponds for frogs and toads are much closer to the beach frequented by these amphibians.

The flora of the low areas, as shown in Figure 3 by small dots, consists of sparse cottonwood stands and sand-reed grass with occasional patches of the prickly pear. Estimates based on several two-thousand-foot transects indicate a per-acre density of twenty to forty cottonwoods with a trunk diameter over four inches. The area is in the early stages of succession.

The higher areas shown on the map have denser cottonwood stands, and many of the trees are larger in diameter. In many places the leaf litter and ground flora indicate somewhat more stable conditions. The older and more permanent ridge (indicated at the eastern edge of the map) contains, in addition, evergreens, cherries and numerous other shrubs. The race runner, *Cnemidophorus sexlineatus,* and the hognose snake, *Heterodon contortrix* (a known predator of the toad), occur up to the northern faces of this ridge.

In Table II it was noted that relative to adult toads, the leopard frog, *R. pipiens,* and small toads are distributed differently along the beach. In the case of the small toads it appears that their numbers along the beach are related to the proximity of the breeding ponds and marshes south and east of the area on the map of Figure 3. Hence their numbers on the beach may be taken as some sort of an index of their dispersion from the areas of their origin. The leopard frog seems to be most abundant adjacent to lower off-the-beach areas. Possibly such areas are more moist because of water closer to the surface, or perhaps frogs are less likely to climb to higher sites for diurnal cover. Not much

information is available for green frogs and bull frogs.

Territoriality has been established for toads and it has been found that toad territories include much less than five hundred feet of beach. Any differences of the toad fauna associated with any particular five-hundred-foot segment of beach may therefore be related to physiographic variations among the beach segments. As noted above under "Toad Density" specimens on the beach adjacent to higher areas have lower plumpness values. It was also noted that significant differences were found in the toad densities among the beach segments. Alone, these density

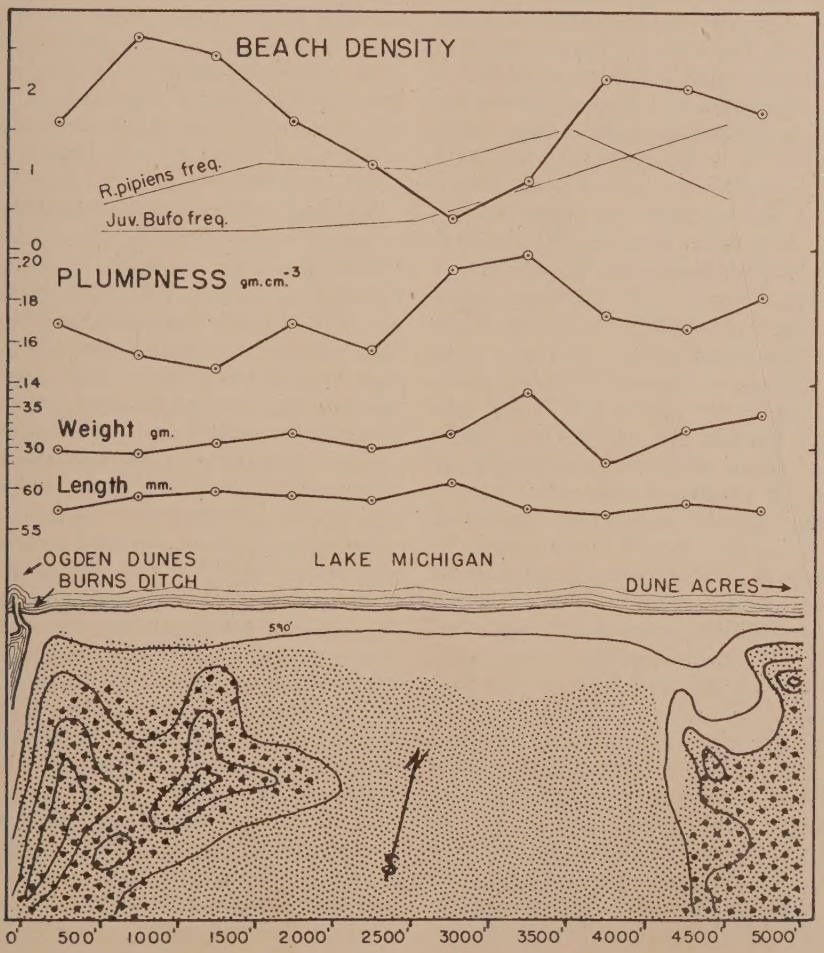

FIG. 3. The relation of beach density (the average number of toads per 500 ft. at any time during the night), plumpness (the relative abundance of body water), weight and length of toads to the physiography of the area studied. The frequencies of *Rana pipiens* and juvenile *Bufo* are comparable to toad densities. The maximum differences in ordinates of the curves reflect the probability of significant differences among the ten beach segments for each variable. (Weight differences are at the five per cent level of significance.) The open areas are loose denuded sand. Small stippled areas are sparse cottonwood stands; the large stipping indicates areas of more dense and older timber. The contour interval is roughly 20 feet.

differences could be taken as an index of varying population density behind the beach, but since the plumpness averages seem to be related to the beach segments in a manner nearly opposite to beach density it is well to consider certain other factors.

Beach density of toads is a measure of the number of animals with similar behavior patterns or motivating stimuli. This beach-frequenting behavior seems to be definitely related to water imbibition and so to plumpness. Figure 3 shows the curves for plumpness and density along the beach. It is apparent that toads tend to have greater beach densities where they have the lowest relative amounts of body water. It remains to relate this observation to local physiographic variations.

It was found in the laboratory that several days of "conditioning" in moist or wet environments were necessary to raise a low plumpness value of a toad to a much higher value (say from 0.1 to 0.2 gm. $cm.^{-3}$). Presumably during this "conditioning" period shifts take place in quantities of the plasma constituents; without sufficient time for such shifts the water imbibed in great excess is eliminated by the kidneys. Specimens obtained from different beach segments with a toad fauna exhibiting consistently high and consistently low plumpness values were found to be in no way different morphologically. Laboratory "conditioning" in wet and dry environments for a period of days resulted in an interchange of the plumpness values of these two groups of specimens. This would lend support to the idea that beach toads with high plumpness values are in general specimens from more moist environments as compared to the beach specimens with low plumpness values.

Sufficient information is not available to interpret local differences in the density of toads on the beach as a measure of either varying local population densities or of local variation in the proportions of physiologically different individuals. It is far simpler to account for these observed heterogeneities in terms of the general needs for toads to replenish body water and to suppose that physiographic features which vary along the beach may affect the rate at which body water is lost. Hence the toads that frequent the beach adjacent to higher off-the-beach areas may live in diurnal microclimates which are drier than those sites occupied by toads found adjacent to low areas. The loss of body water is expected to be greater in drier sites. It would seem that the more frequent replenishing of body water is necessary to survival in the higher areas and so beach density reflects relatively greater needs for water.

Rising plumpness values of toads imbibing water in the field may well modify behavior, as seems to be the case in the response of leaving the beach (prior to sunrise). On three occasions in 1946 and 1947 a passive toad was watched in moonlight or subdued artificial light. In each case the toad was so situated that waves occasionally surged up to the animal's position, requiring it to relocate itself. Eventually each toad left the beach following a wave incident such as this. The handling of toads in the field provides a stimulus to which three-fourths of the specimens respond by immediately leaving the beach. All specimens whose home territory was revisted within an hour after initial capture and release were considered to be potential recaptures (and indicated by a dot in Figure 2). Of 48 potential recaptures, one was made among the 18 specimens with plumpness values greater than 0.16; 11 recaptures were made among the 30 specimens with plumpness values less than 0.16. It is interesting to note that in spite of the artificiality of this situation, a lower plumpness value seems related to a greater likelihood of a toad remaining longer on the beach and imbibing water (on any particular night).

Additional evidence for the modification of behavior as related to the relative amount of body water is to be had from data collected in 1950. During the fall season of this year shoreline erosion pro-

duced an abrupt "step" varying from more than a foot to four inches at the water line in most places along the beach. Where this step occurred (locally termed "sea wall"), the usual wet sand strip was absent, and tracks indicated that toads often toppled over the edge and fell into the lake. These toads apparently find low places along the step and again regain access to the beach. Many toads stop at the edge of this step; frequently the splashing of the waves moistens this step. One of the few specimens tagged was first encountered while it was enroute to the beach. Seven and one-half hours later it was found on the moist sand of the step; its tracks indicated that it had been there for the entire time. Its plumpness gain was typical of specimens on wet sand for about two hours. The extreme duration of the stay on the beach by this specimen may be explained by the slowness of the plumpness rise. If this is the case the unusually larger number of toads present at this time would be due to earlier arrivals remaining longer on the beach rather than being succeeded by the later arriving toads. The halting response, elicited by moist sand (or perhaps previous experience in falling over the step), resulted in arraying most toads on the step where water imbibition is presumably retarded. Since the conditions had changed, the data for 1950 are not wholly comparable to those of 1948–9, but these data further emphasize the connection of nocturnal behavior to body water and water imbibition and survival in rather arid situations.

Of the frogs and toads studied by Thorson and Svihla (1943) *Bufo terrestris* is ecologically closest to *B. fowleri*. They found that *B. terrestris* could survive losses in body water as high as 43 per cent of the initial weight. Plumpness changes in *B. fowleri* from 0.23 to 0.08, produced in the laboratory by slow drying, correspond to a loss of 65 per cent of the initial weight. No effort was made to duplicate the conditions for water loss used by these workers; hence, these data are not comparable. Their data were collected at much higher rates of dehydration. However, since individuals of the aquatic forms *R. clamitans* and *R. catesbeiana* and the semi-aquatic *R. pipiens* are able to occupy the arid habitats with the toad, one is inclined to speculate that the capacity for water loss in amphibians may be less important than their adaptability of behavior in the conquest of dry land.

Toad plumpness is probably related to temperature as is the case in frogs when cooler temperatures result in greater retention of absorbed water (Ott 1924). Greater plumpness values after cool weather may, however, be due to suppression of evaporation rates, rather than to physiological changes of the toad.

Steen (1929) has shown that the bladder of *Rana pipiens* may act as a water reservoir, the water being reabsorbed during periods of drying. No doubt this is true in the case of toads, for specimens found in early morning behind the beach usually void water when handled. Presumably these specimens had visited the beach on the previous evening.

Qualitative agreement between density and evening dew point or air temperatures is discernible. These yield a curve that matches the troughs and crests of the density curve of various dates, but this leaves much to be desired. Directions of change in daily maximum, minimum, and average temperatures are reflected in the plumpness data but the relation is similarly weak. Air temperature seems to affect behavior slightly as it is manifested by beach occurrence, but if nothing more, it at least inhibits such occurrences in the range of 15° C. and lower.

This information on the apparent independence of amphibian behavior of climatic factors could thus be taken to indicate that the typical diurnal habitat of the animal is out of reach of small fluctuations. Plumpness values, though variable, appear unrelated to rain and humidity effects. The small variability ex-

plained by temperature may mean more successful feeding.

Toads caught at night and released in sunlight hastily disappear by digging into the sand. Of the adult *Bufo* found in late summer on sunny days, half hopped out of shallow excavations near sticks, clumps of grass, and so forth. Another sat in the opening of a horizontal hole in a fairly steep slope of sandy prominence. Others were found under logs, debris, and the like. All of these specimens were noted in early morning at various dune localities far from the beach. After noon, the only adult *Bufo* ever taken were recovered after they fell from the walls of holes in which cooking fires were being kindled. Several additional young toads were also collected in this way. Hence, if the typical diurnal sites of *Bufo* are some sort of excavations, probably newly dug, most of the daily weather effects would not be influential on behavior. (Even the effects of heavy rains are apparently not especially important.)

Considering the above facts, it would seem that the Dunes toad, after nocturnal activity, digs or returns to some sort of a retreat and for much of the early morning remains near the surface, probably feeding on whatever happens to move within reach. As the hotter period of day approaches the animal may dig further if necessary. Several days or more could be spent in this way. (Table I, at face value, would indicate an average frequency of one trip to the beach every four or five days. However, nothing would prevent a toad from moving about without being seen on the beach.) A declining plumpness value mainly due to slow water loss might then produce the behavior that again results in the animal appearing on the beach. We can understand the variable time of beach appearance of particular individuals on different nights by assuming that toads occupy different locations for diurnal habitats, and thereby require varying amounts of time to travel to the beach. Variability of time of appearance could also result from digging to different depths and so being stimulated to activity by the changing phenomena associated with sunset either not at all or at varying times during the night. This qualitative activity pattern is wholly consistent with the activity polygon determined mechanically in the laboratory for one toad, presumably from this area, over a period of ten days (Higginbotham 1939).

Some estimates of growth are available for the toad, *Bufo fowleri*. Information on growth rates for toads larger than 50 mm. is derived from data on changes in length (snout to end of urostyle) of tagged individuals. For smaller toads, modes of frequency distributions are taken to be indicative of the length of size groups originating in consecutive years. A composite scheme follows: at the end of the first season the juveniles are about 40 mm.; at the end of the second season these toads are expected to be about 50 mm. (possibly some of the larger individuals of this group would breed in the following season). For toads over 50 mm. in length the annual growth increment varies from over 4 mm. to about 1 mm. for specimens 60 mm. and over. No doubt certain individuals depart greatly from this scheme—the 72 mm. specimen (Table I) was probably much less than ten years old.

Acknowledgments

Although many persons have been quite helpful during the course of this study, the writer wishes to acknowledge the following persons in particular. Familiarity with the area and its fauna and flora dates back to the early 1940's and the many field trips with E. J. Lace and E. J. Tierney. My wife, Lois, aided in the later field work. With the help of Jiro Ishihara the map of Figure 3 was drawn; the preparation of the manuscript was aided by Mrs. Stille, S. E. Tarbox, and Mrs. S. A. Tedor. K. P. Schmidt, C. H. Pope, Sewall Wright, and H. K. Gloyd, as well as fellow students, have made suggestions and criticized the outcome and

methods of this study. Their help is greatly appreciated.

Conclusions

Bufo w. fowleri, Rana catesbeiana, R. clamitans, and *R. pipiens* are members of the nocturnal amphibian beach fauna of Southern Lake Michigan.

Tag effects on toads such as higher mortality, an impediment to feeding, and so forth, appear to be absent. Jaw tags are not permanent.

The relative excess or deficiency of body water may be assessed by the ratio (termed "plumpness") of the weight in grams divided by the cube of the length in centimeters.

Body water is replenished by amphibians on nocturnal visits to the beach; it is imbibed by toads by passively sitting within the wet sand strip and by frogs by entry into the Lake. Feeding, if at all general, is an unimportant factor in these visits.

Water seems to be imbibed by toads primarily through the skin of the groin area.

The feet of the toad are sensitive either to moisture or to differences in packing between wet and dry sand.

Light intensity seems most closely related to amphibian beach appearance and disappearance. Thus sunset time provides a better base for reference than standard time (based on the sun at zenith).

The "home range" of the toad includes much less than 500 ft. of beach. *R. catesbeiana* may have similar territories; information on territoriality of the other frogs is wanting.

Frogs appear most abundant adjacent to areas at low levels; presumably such areas do not necessitate a climb to diurnal sites and presumably the lower sites are more moist.

Juvenile toads are more abundant on the beach adjacent to the areas of their origin.

Adult toads appear in greatest numbers on the beach adjacent to high (drier) areas in comparison with low (more moist) areas. Plumpness values are inversely related to the elevation of the area behind the beach. This is interpreted in terms of the amount of water necessary for survival; frequenting the beach for water seems to be more often necessary in drier areas where body water loss through evaporation is greater. Toads of low areas carry excess weight attributable to excess water, and so they seem more independent of the water needs than toads of higher areas.

Toad behavior related to the length of stay on the beach, and possibly that related to frequency of beach appearance, seems to be modified by the relative amount of body water.

The late summer toad activity cycle seems to be: after imbibing water on the beach, a toad returns to diurnal sites before sunrise; remaining near the surface, it feeds on anything coming within reach; as hotter daylight hours approach it may dig or descend farther below the surface; body water is replenished once in about five days.

Nightly beach appearance tends to be earlier in areas where toads are lighter in weight (*i.e.,* relatively deficient in body water), vegetation is closer to the beach, and the slope of the beach is steeper.

Climatological effects are obscure. Air temperatures lower than 15° C. appear to inhibit beach appearance. Cool evenings are correlated with the tardy appearance of the first amphibians.

Toads may reach a length of about 40 mm. in their first year of life; at the end of their second year they are about 50 mm. long. The annual growth increment thereafter varies from over 4 mm. to 1 mm. for toads larger than 60 mm.

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PHOTOSYNTHESIS AND GROWTH RATES OF TWO DIATOM COMMUNITIES IN WESTERN LAKE ERIE

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INTRODUCTION

During 1949 a year-round study was made of the photosynthetic activity exhibited by phytoplankton communities inhabiting the waters of the western Lake Erie island region. One conclusion from that study (Verduin 1951b) was that the different species which have become adapted to a particular aquatic habitat show remarkable similarity in photosynthetic rates. In the spring months of 1950 an *Asterionella-Cyclotella* community was observed in the waters around Pelee Island and at the same time a *Stephanodiscus* community was found about 20 mi. east of Pelee Island. The presence of these distinctly different communities afforded an excellent opportunity to study them simultaneously, using samples collected from each community on the same dates. Their photosynthetic rates, growth rates, and related characteristics are described and discussed below.

METHODS

A mobile sampling method previously described (Verduin 1951a) was used in collecting samples. Surface samples were collected at one-half hour intervals on each sampling trip; the boat cruised at about 10 mi. per hour. The phytoplankton was removed by filtering a measured volume of water through No. 25 silk bolting cloth and washing the plankton from the filter with a measured volume of the water which had passed through the filter. The volumes of water were calculated to provide the concentrations of diatoms necessary to facilitate photosynthesis measurements, about 10^{11} μ^3/l. The degree of concentration to which natural populations were subjected varied from 10-fold for peak populations to 100-fold for low populations.

The method of measuring photosynthesis has also been described previously (Verduin 1951b). It consisted of making pH determinations (Beckman meter) at the beginning and end of a period during which the diatom suspensions were exposed to fluorescent light of about 400 f.c. The flasks containing the diatoms were submerged in a tray through which lake water flowed, thus maintaining the temperature near that of the natural environment. The pH change observed provided an estimate of CO_2 absorbed during the test period. Respiration rates were similarly determined by subjecting the samples to a period of darkness after the photosynthesis tests were completed. The nomograms published by Dye (1944) are useful in applying this method.

The volume of diatoms contained in a sample was estimated by counting 10 fields in a Sedgewick-Rafter cell, and making 3-dimensional measurements of the abundant species (Welch 1948).

Ash-free dry weight of samples was determined by igniting oven-dry samples in porcelain crucibles over a carbon-free gas flame. Weight before and after ignition was determined on a "Chainomatic" balance.

In plotting growth curves species composition of the samples was used to indicate the community to which a sample belonged, and the 3 consecutive samples yielding the highest average standing crop were combined to represent the population density of a given community on a given sampling date. In this way samples influenced by mixing at the edges of the communities were not allowed to affect the shape of the curves.

The light penetration data reported below were obtained with a Weston photronic cell enclosed in a water-tight case,

the same instrument used by Chandler (1942). Turbidities were determined by measuring light transmission of water samples with a Coleman spectrophotometer (set at λ 720) and reading p.p.m. turbidity from a calibration curve obtained by using a suspension of diatomaceous earth.

Results

Photosynthetic rates as determined by laboratory tests

The photosynthetic rates exhibited by the *Asterionella-Cyclotella* community and those of the *Stephanodiscus* community appear in Table I. The μ moles of CO_2 used by 10^{10} μ^3 of the *Asterionella-Cyclotella* community per hour was 1.7 times the rate observed for the *Stephanodiscus* community. The possibility that volumetric measurements of diatoms might be deceptive was recognized (unit volumes of different species might represent radically different amounts of protoplasm). Therefore the photosynthetic rates were also computed on an ash-free dry weight basis. On this basis the *Asterionella-Cyclotella* community rate was 2.2 times that exhibited by the *Stephanodiscus* community. The respiration rate of the *Asterionella-Cyclotella* community also was higher (2.3 times) than that of the *Stephanodiscus* community. The ratio of respiration to photosynthesis, however, was practically the same in both communities.

Table I. *Comparison of an* Asterionella-Cyclotella *community with a* Stephanodiscus *community*

Characteristic	Community	
	Asterionella-Cycloiella	*Stephanodiscus*
Photosynthetic rate (μ moles CO_2 used/10^{10} μ^3 of diatoms/hr.)	2.12	1.22
(μ moles of CO_2 used/mg. of ash-free dry weight/hr.)	0.70	0.34
Respiration rate (μ moles of CO_2 evolved/mg. of ash-free dry weight/hr.)	0.16	0.07
Ratio of respiration to photosynthesis	0.23	0.21
Ash-free dry weight per unit volume (mg./$10^{10}\mu^3$)	3.0	3.6

Data in the second column are averages of 21 samples, in the third are averages of 17 samples, taken on 5 sampling trips: April 18, 27, May 1, 5, and 11. Photosynthesis rates are corrected for respiration. Differences between communities in photosynthesis and respiration rates are highly significant.

The shapes and sizes of the cells comprising each community presented a striking contrast. The *Asterionella* cells were about 80 μ long by 3 wide and 3 deep, thus having a volume of 720 μ^3 and an area of 720 μ^2. The *Cyclotella* cells were cylindrical having a diameter of about 12 μ and a height of 12 μ, thus having a volume of about 1350 μ^3 and an area of 680 μ^2. *Stephanodiscus* cells were also cylindrical but had a diameter of 80 μ and a height of 35 μ. Their volume then was 175,000 μ^3 and area about 19,000 μ^2. The volume of a *Stephanodiscus* cell was 100-fold greater than that of *Asterionella* or *Cyclotella* cells. The ratio of volume to area in an *Asterionella* cell was 1.0; in a *Stephanodiscus* cell this ratio was 0.09; therefore a unit volume of *Asterionella* protoplasm, in absorbing materials from its environment, had 11 times more exposed surface than did a unit volume of *Stephanodiscus* protoplasm.

These contrasting characteristics of the two communities are so far out of proportion with the 2-fold differences appearing in Table I that they are probably not operative in determining the photosynthetic and respiratory rates presented there. Moreover, the fact that both photosynthesis and respiration rates of *Stephanodiscus* equal approximately one-half the rates of the *Asterionella-Cyclotella* community suggests that the *Stephanodiscus* cells have about one-half as much active protoplasm as the *Asterionella* and *Cyclotella* cells. But the *Stephanodiscus* cells have somewhat more ash-free dry weight per unit volume, so the non-active fraction probably represents stored materials. The greater amount of stored material apparently present in *Stephanodiscus* cells may be the most significant difference between these two communities.

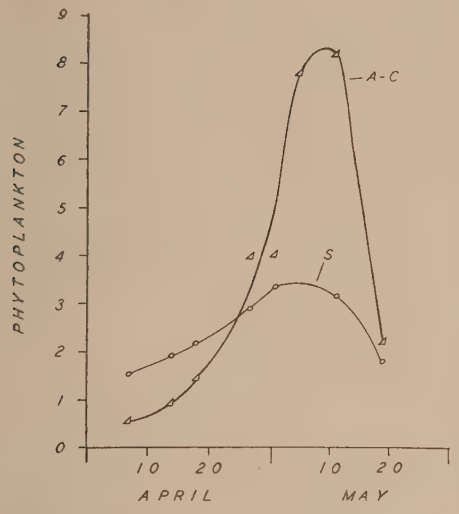

FIG. 1. Phytoplankton volume per liter ($\mu^3 \times 10^{-10}$) on successive sampling dates in 2 communities growing in western Lake Erie. Each datum-point represents the 3 consecutive samples yielding the highest average for the community on that sampling date. A–C is the *Asterionella-Cyclotella* community, S is the *Stephanodiscus* community.

Growth rates as determined from the population densities observed on successive sampling trips

In Figure 1, the population densities observed on successive sampling trips are plotted for each community. The points lie fairly close to the smooth curves drawn through them. In this respect they present a contrast to much of the data appearing in the literature which, as has been pointed out before (Verduin 1951a), is frequently so erratic that smooth curves cannot be drawn through the datum-points. The first part of the *Asterionella-Cyclotella* curve lies below that of the *Stephanodiscus* curve but the *Asterionella-Cyclotella* community multiplied more rapidly and reached a higher peak than the *Stephanodiscus* community. The population peaks were attained at about the same time in both communities, so apparently the factors influencing the beginning and duration of the growth phase were common to both communities. Figure 2 shows the datum-points appearing in the growth phases of the Figure 1 curves plotted on a logarithmic ordinate. The data exhibit a straight-line relationship in this graph, indicating that growth rates in each community were fairly constant during the growth phase. The rate in the *Asterionella-Cyclotella* community, however, amounted to a doubling of the population every 7 days, while the *Stephanodiscus* community doubled only once in 23 days. It is evident that the community which showed the lower photosynthetic rate in laboratory tests (Table I) also showed the lower growth rate under natural conditions. The proportions are not identical; the photosynthetic rates were in a ratio of approximately 2 : 1 while the growth rate ratio was more nearly 3 : 1.

Comparison of two independent estimates of photosynthesis

The growth rates portrayed above can be used to provide estimates of photosynthesis quite independent of the rates measured in the laboratory, but a fair approximation of the thickness of the illuminated water layer in each community (euphotic zone) is necessary

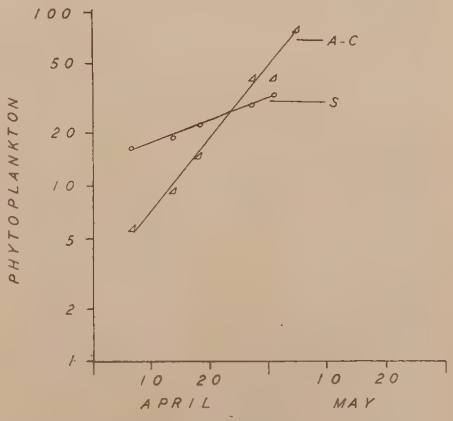

FIG. 2. Data from the growth phase of the pulses shown in Figure 1 graphed on a logarithmic ordinate ($\mu^3 \times 10^{-9}$/l.). The *Asterionella-Cyclotella* line (A–C) indicates a doubling of the population every 7 days; the *Stephanodiscus* population (S) doubled only once in 23 days.

before the estimates can be made. Chandler (1942) has discussed some of the aspects of turbidity as related to light penetration in western Lake Erie. But he does not portray, quantitatively, the relation between turbidity and the thickness of the euphotic zone. During 1949 measurements of turbidity were made at approximately biweekly intervals at 2 stations near Put-in-Bay. Light penetration was also measured at the same place and time that the samples were collected for turbidity determination. An analysis of these sets of data yielded the relationship shown in Figure 3. The depth at which light intensity equalled 1% of surface light is plotted against turbidity. Each point represents the average of 3 turbidity determinations (0-, 5-, and 9-meter depths) and a curve has been drawn through the scatter diagram. This graph makes it possible to estimate the thickness of the euphotic zone from a knowledge of the turbidity in a community.

In studying the two communities described above the turbidity of surface samples was determined routinely. The average turbidity in the *Asterionella-Cyclotella* community was 15 p.p.m.; in the *Stephanodiscus* community it was 7 p.p.m. These values are marked by arrows labelled A-C and S in Figure 3. Although the depth of the water in the *Stephanodiscus* community (18 m.) was about twice that in the *Asterionella-Cyclotella* community (8 m.), the euphotic zone represents about one-half the water column in each community.

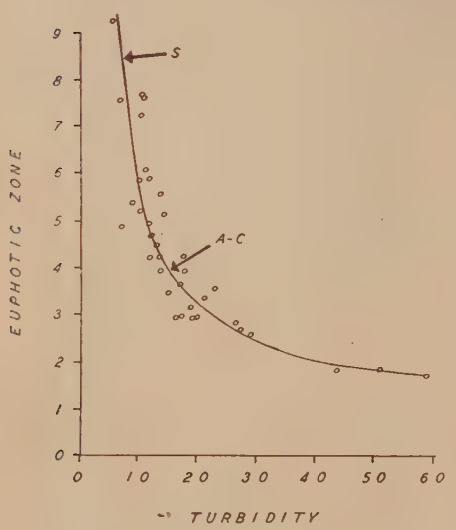

FIG. 3. The depth, in meters, to which 1% of surface light penetrates (thickness of euphotic zone) graphed against turbidity in p.p.m. Arrows compare the average conditions in the *Asterionella-Cyclotella* community (A–C), during the period of this study, with those in the *Stephanodiscus* community (S).

This estimate of thickness of the euphotic zone in each community permits a deduction of the photosynthetic rate represented by the growth rates appearing in Figure 2. The doubling of a population in 7 days represents a synthesis of 1 mg. of organic matter per mg. of diatom protoplasm per 7 days for the *Asterionella-Cyclotella* community. The doubling of a *Stephanodiscus* community in 23 days represents synthesis of 1 mg. of organic matter per mg. of *Stephanodiscus* protoplasm per 23 days. Assuming 12 hours of illumination per day, and noting that in both communities one-half of the water column is illuminated, it appears that the diatoms are subjected to an average of 6 hours illumination per day. But if a correction is to be made for respiration the estimate of photosynthesis will probably have to be doubled since the average time in darkness is 3 times the amount spent in the light. The growth rate in the *Asterionella-Cyclotella* community, therefore, represents a photosynthetic rate of $(2/7 \times 6)$ 0.048 mg. of organic matter per mg. of diatom protoplasm per hour. The photosynthetic rate reported in Table I was 0.76 μ moles of CO_2 used per mg. of ash-free dry weight per hour, which corresponds to 0.023 mg. of glucose. The growth rate of the *Stephanodiscus* community represents a photosynthetic rate of $(2/23 \times 6)$ 0.014 mg. of organic matter per mg. of diatom protoplasm per hour. The photosynthetic rate reported in Table I was 0.34 μ moles of CO_2 used per mg. of ash-free dry weight per hour which cor-

responds to 0.010 mg. of glucose. The discrepancy between these independent estimates is not large, considering the roughness of the approximations used. The fact that the estimates based on growth rates are higher in both cases than the rates observed in the laboratory suggests that the average photosynthetic rate in the euphotic zone may be higher than the rate observed under 400 f.c. fluorescent light.

Discussion

The conclusion made from the 1949 study, that communities adapted to a particular aquatic habitat are similar in photosynthetic rate, is supported by the 1950 data. The average photosynthetic rate of the *Asterionella-Cyclotella* community (2.12 μ moles $CO_2/10^{10}$ μ^3/hr.) is very close to the rate exhibited by communities inhabiting the waters of the island region during 1949 (1.7 μ moles $CO_2/10^6$ standard units/hr.; the unit used then was 8,000 μ^3). The comparison of the *Stephanodiscus* community with the *Asterionella-Cyclotella* community, however, indicates that communities which are adapted to different aquatic environments may have distinctly different photosynthetic rates per unit of plant volume.

It is interesting that the community associated with the deeper water exhibited the lower photosynthetic and respiratory rates, characteristics which suggest the presence of stored materials. It is possible that diatom cells in the deeper water are subjected to longer periods of starvation than those in the shallower water and that stored materials have important survival value in such an environment. Since the euphotic zone in both communities occupied about one-half of the water column the longer starvation periods postulated could only result from a lower water exchange rate between the upper and lower half of the water column in the deeper habitat. It would be profitable to know how much time a diatom cell spends in the euphotic zone (on the average) before it is again carried down into the darkness. That is, does the 6 hours per day used in the calculations above represent a single trip per day, or more, or less? Undoubtedly the time period spent in the euphotic zone varies considerably under varying conditions of wind and current, but at present even its order of magnitude is unknown. A study of vertical turbulence in the island region and in the waters 20–30 miles to the eastward might yield some pertinent information.

The measurement of growth rates as described above assumes that loss of phytoplankton to grazing herbivores is negligible. The good fit of the data to a straight line in a semi-log graph (Fig. 2) supports such an assumption since it seems unlikely that a grazing population would take a constant fraction of an exponentially increasing plant population. The fact that photosynthetic rates based on observed growth rates were higher than the rates observed in the laboratory also supports the assumption, for, if an important fraction of the photosynthetic yield were diverted to grazing herbivores, one would expect the CO_2-uptake-based yield to exceed the growth-based yield. It is noteworthy that Lund (1950) studying *Asterionella* in English lakes regularly obtained straight-line plots on semi-log graphs, and also concluded that grazing was negligible. Lund did not discuss growth rates but the slopes of the plots show that the rates varied from year to year, between limits which appear to represent a doubling of the population in 4–10 days. The photosynthetic activity represented by such growth rates would be similar to that exhibited by the *Asterionella-Cyclotella* community and other communities inhabiting the waters of the Lake Erie island region. The growth rate of the *Stephanodiscus* community described above, however, was lower than the lowest appearing in Lund's report.

Summary

Comparison of an *Asterionella-Cyclotella* community with a *Stephanodiscus* community growing in western Lake Erie

showed that the photosynthetic rate and respiration rate of the former were approximately twice those of the latter. The natural growth rate of the *Asterionella-Cyclotella* community was about 3 times that of the *Stephanodiscus* community. Although the *Stephanodiscus* community grew in water having a depth (18 m.) about twice that of the *Asterionella-Cylotella* habitat (8 m.), the euphotic zone represented about one-half the water column in both communities, because the water in the *Stephanodiscus* community was less turbid (7 p.p.m.) than in the *Asterionella-Cyclotella* community (15 p.p.m.). It is suggested that *Stephanodicus* cells may have less active protoplasm per unit volume than *Asterionella* and *Cyclotella* cells have, the non-active fraction perhaps representing stored materials, and that this may be the most significant difference between the communities. If *Stephanodiscus* cells are subject to longer periods of starvation than the cells growing in the shallower waters of the island region, this situation can be caused only by lower exchange rates between the upper and lower halves of the water column in the deeper habitat. Grazing by herbivores appears to be negligible in western Lake Erie during the spring phytoplankton pulses.

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ECOLOGICAL ASPECTS OF DISPERSAL OF THE SNAIL *CAMPELOMA DECISUM*

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The occurrence of animal aggregations in the field invariably piques the ecologist's curiosity. Two problems are raised. What are the environmental actions and what are the responses of the population resulting in the aggregation phenomenon? The finding of such an aggregation of snails in a small Michigan stream prompted the investigation of these problems. At one point the bottom of this stream was actually blanketed by snails of the species *Campeloma decisum* Say. Any one handful of the substratum material yielded tens of snails in addition to the sand and gravel. This paper will report first on a survey of population size at various transects of the stream and secondly on experimental analyses of the reaction of the snail population to critical environment actions.

The valuable and generously given assistance of Henry Van der Schalie, of the University of Michigan, in checking identifications is gratefully acknowledged. Sample specimens are deposited in the Museum of Zoology, University of Michigan. I am indebted further to my colleague, H. D. Stalker, for a helpful reading of the manuscript.

POPULATION DENSITY ESTIMATES

Description of study site

Dickerson Creek, the stream investigated, is in Montcalm County of central Michigan. The particular site is five miles east of Greenville, approximately midway between the source and confluence with the Flat River. The region is gently rolling, the stream having cut a broad valley between gravel hills overlaid with clays. Silt depositions have resulted in extensive marginal swamps. Gallery forest is of second growth mixed hard and soft woods; the entire course of the stream is wooded. The surrounding area is largely agricultural.

At the study site the creek flows all year, fed by small springs and tributaries. Summer waters are of wading depths but spring floods increase this greatly. Riffle stretches alternate with deeper pools. In this region of the stream the substratum is almost entirely of coarse gravel and sand with scattered stones and boulders. Depositional margins are silted and the entire stream bed is littered with logs, branches and more minute detritus. The clear water is well aerated and relatively unpolluted. Rate of flow in summer is moderate, approximately one-half meter per second in rapid water. Spring and occasional flash floods increase this rate many times. Oxbows and quiet backwashes contain emergent vegetation. Several species of algae inhabit marginal and submerged wood and stone. The general fauna is characteristic of such streams. The major alteration of the environment is the impounding of the stream by a small dam a short distance upstream of the initially observed snail aggregation (see Fig. 1).

Population sampling procedure

The snail population was sampled at eleven transects. A metal frame enclosing an area of one-fourth square meter was dropped on the bottom and the quadrat thus defined. From five to nine such quadrats comprised a transect sample, depending on stream width. The bottom materials and the contained snails were worked over by hand, the snails sifted out, and numbers recorded. *C. decisum* was the only snail present at the time and particular area of the study.

The size of the individuals fell into the categories of young and adult. These

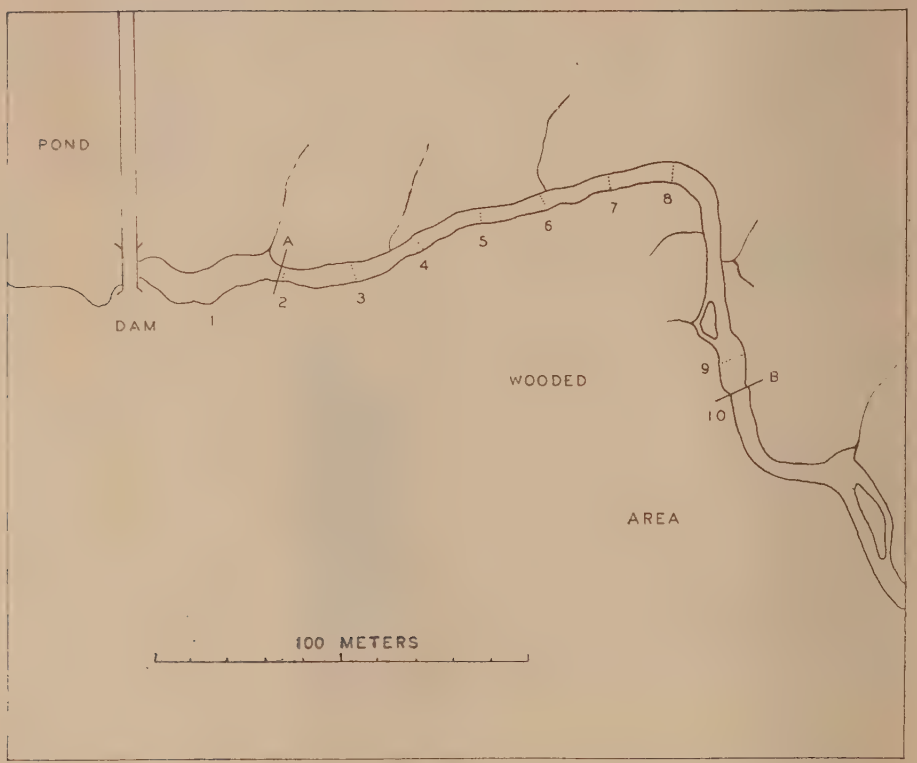

FIG. 1. Dickerson Creek at the point of study; numbers indicate stations where population density samples were taken; letters designate two rapids.

data are in agreement with those of Van Cleave and Altringer (1937) on *C. rufum* in Illinois. They report tri-modal distribution of summer shell height corresponding to the spring brood and the one- and two-year-old adults. In the present investigation the spring brood of very small snails was not recorded since an accurate sample of the young would be very difficult to obtain and the purpose of the study was to secure comparative rather than complete samples.

Results

At any one transect, substratum conditions were variable and population density varied. Density tended to be higher marginally in the areas of less current and in the presence of silt and detritus. These data corroborate those of Allison (1942) who notes the "frequenting of shallow, mucky situations."

Two transects were sampled for a preliminary study, one at the point of the initially observed aggregation and the other approximately 500 meters downstream. The population density decreased in this distance from a mean of 607 snails per quadrat (ranging from 71 to 1728) to 9 snails per quadrat (ranging from 0 to 23). An attractive hypothesis was formulated: population density varies inversely with the downstream distance from the point of artificial impounding of the stream. This would appear to be related to the diminishing food supply, characteristic of such impounded streams.

Data from systematic sampling, at 20-meter intervals from the foot of the dam downstream 200 meters, negated this hy-

pothesis. Two population peaks were located, one 40 meters below the dam at station 2 and another at 200 meters, station 10 (Fig. 1). While the originally observed aggregation was determined to have a mean population density of 607 snails per quadrat, 20 meters upstream this density dropped to 6 snails per quadrat (ranging from 0 to 20). This is a decrease of one-hundred-fold. Down stream the numbers decreased as well but far less precipitously; in successive transects at 20-meter intervals the mean densities per quadrat were 297, 147, 112, 67, 41, and 36 snails. At 160 meters downstream the count was reduced to 3 snails per quadrat (ranging from 1 to 6). However, 10 meters below this lowest recording, a new aggregation was found with a population density of 243 snails per quadrat (ranging from 111 to 408). The results of these samplings are recorded in the histogram of Figure 2 and clearly demonstrate other factors than downstream distance from the impoundment acting to create the aggregations.

Reactions to Two Physical Factors

At each point of population peak the snails were crowded against an upstream physical barrier. These were composed of boulders and logs jammed across the stream and backed up by smaller rocks, gravel, and branches. The water flowed over them with a drop of a few inches. Since the water was generally well aerated and rapidly flowing, little difference in gas content could be postulated. No differences in the general biotic composition were observed. The physical blocking of upstream movement of the snails seems the most likely environmental factor acting to create the high population densities at these points. Experimental investigations were designed to test (1) the reaction of *C. decisum* to water movement and (2) reaction to a physical barrier.

Reaction to water movement

In an experiment testing reaction to water movement, snails were released at the midpoint of a long wooden chute

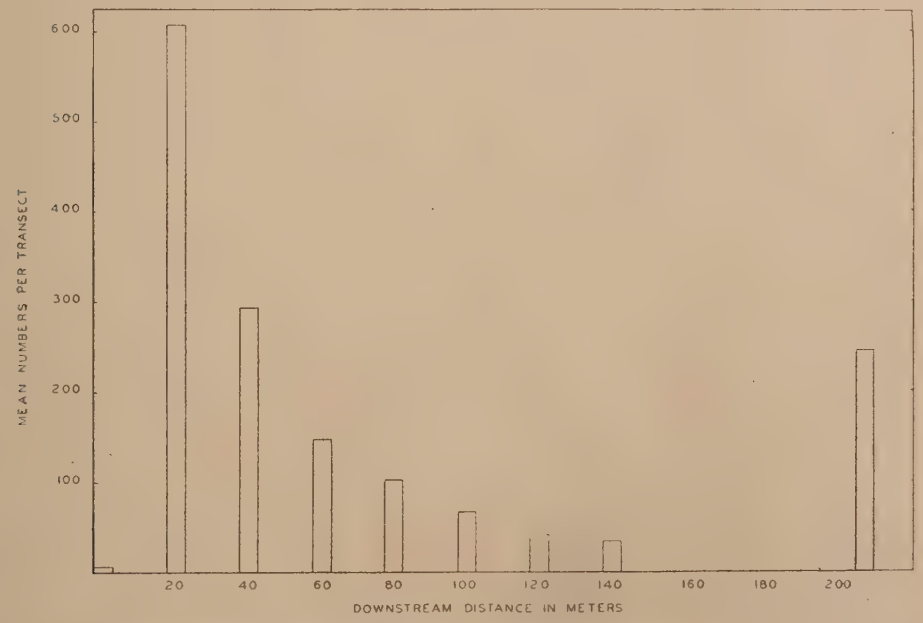

FIG. 2. Mean numbers of snails per transect at the stations sampled in a 200-meter stretch of Dickerson Creek.

TABLE I. *Rheotactic response at two rates of current as measured by numbers recovered above and below the midpoint of the experimental chute (24 hours after release)*

Water flow of 25 cm./sec.			Water flow of 5 cm./sec.		
Experiment	Positive	Negative	Experiment	Positive	Negative
a	98	2	a	94	6
b	96	4	b	78	22
c	85	15	c	83	17
d	73	27	d	87	13
e	82	18	e	89	11
f	78	22	f	96	4
Sum	512	88	Sum	527	73
Mean	85.33	14.67	Mean	87.83	12.17

placed in the stream bed. They were recaptured after a twenty-four-hour period and their position in the chute was recorded.

The experimental chute was seventeen meters long, twenty centimeters wide and water depth in the chute was approximately ten centimeters. The ends were screened. The bottom was covered with sand and gravel simulating natural physical conditions, but stream animals other than planktonic were excluded and algal growth controlled. Rate of current was regulated by partial blocking or funneling at the upstream end. The length of the chute was calibrated in segments of one meter, numbered positively from the midpoint upstream and negatively downstream.

One set of 6 replicate experiments was conducted with a mean rate of current approximating 25 cm./sec., corresponding roughly to that of the adjacent stream. A second set of 6 experiments was performed at near 5 cm./sec. mean rate; such a slow rate is characteristic of only the most quiet reaches of the stream. Current was measured by timing a weighted cork for the course. For each of the 12 experiments, 100 snails were procured from the stream and marked with red lacquer. The experimental population was placed in the chute; observations were made at frequent intervals in the subsequent twenty-four hours. At the end of this period all were recovered by carefully sifting the substratum in each meter segment. Since the population was in a closed environment all 1200 marked snails could be located precisely and recorded.

A definite and consistent upstream movement was observed. Reaction to current was regular after the first hour; the faster-moving snails proceeded upstream at a rate of 8 meters per day. Twelve-hour recordings of approximately 4 meters for the more rapidly moving individuals corroborate this rate. Table I, recording numbers of snails recovered above and below the release point, indicates the regularity of positive reaction of the large group. Table II, showing the breakdown by segment, reveals a large number moving rapidly upstream but others apparently moving less rapidly or more random in their orientation. Some of those recovered in downstream segments were carried by the current but some were observed to burrow downstream in the substratum.

The experimental chute had an inclination corresponding to that of the stream at that point; this difference in level was approximately 5 mm. per meter of chute. Therefore, a slight gravitational gradient was present. The reaction of the experimental snails could not only have been positively rheotactic but also geotactic or

TABLE II. *Distribution of snails within the experimental chute after a 24-hour period*

Numbers are totals of 6 replicate experiments at 25 cm./sec. and 6 at 5 cm./sec. Release point was at 0; direction of water flow was from left to right.

Meters	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	total
25 cm./sec.	122	125	18	17	34	71	49	55	21	35	21	10	4	6	6	3	1	2	600
5 cm./sec.	181	126	72	23	23	40	24	13	25	18	5	11	10	16	5	2	6	0	600

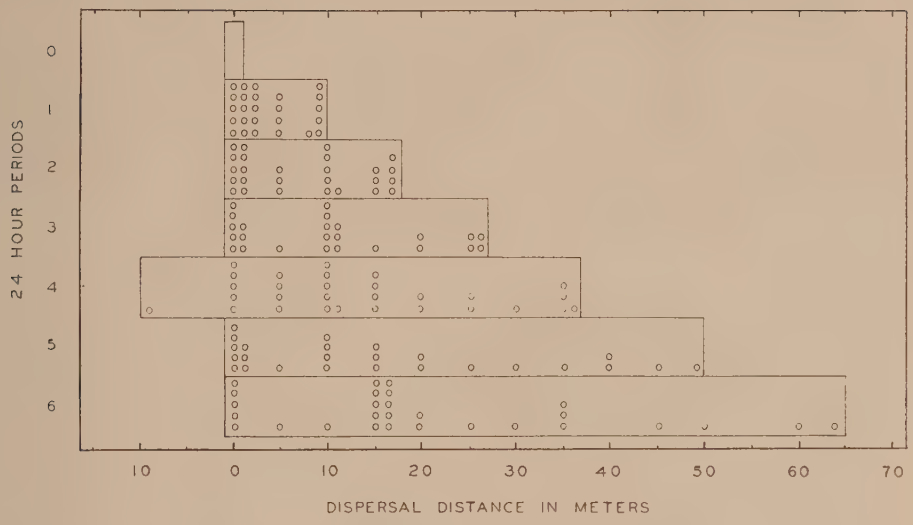

FIG. 3. Dispersal pattern of snails recaptured over a period of six days. Each circle represents one marked snail at the point of recovery. Release point at 0 meters; water flow from right to left.

a combination of these. A further set of experiments and controls was performed with gravitational gradient as variable.

A shorter, 4-meter chute of similar construction was placed at right angles to the stream axis. Current was eliminated. Eight replicate sets of 40 snails were tested by the release-recapture techniques previously described. One-half of these were tested with the chute level, the other half in the chute with a drop of 10 cm. in 4 meters.

In both level and tilted chutes the percentage dispersing towards the two ends was essentially equal. In each case approximately 50 per cent remained within one-half meter of the release point; the remaining snails were equally distributed in the two ends of the chute. The tendency was apparently to move randomly near the release point with but a few wandering to the ends of the chute. The trails left in the sand tend to support this view. The subjective impression was of less movement than in flowing water.

Release and recapture under natural conditions

To corroborate under natural conditions the extent to which the experimentally demonstrated rheotaxis occurs, 500 marked snails were released in a characteristic reach of the stream. At twenty-four hour intervals over six days, transects at 5-meter intervals above and below the release point were sampled for the presence of marked snails. A search was made to a distance of 20 meters upstream and downstream of the area occupied by recovered, marked snails. After being recorded these snails were left in the same position and orientation to the water movement.

The same upstream movement was noted in these observations as was recorded in the previous experiment. Dispersal rate as measured by the leading animal was very regular. The foremost marked specimen moved upstream at the rate of approximately 10 meters per day. This is of the same magnitude as that displayed by the snails in the experi-

TABLE III. *Duplicate experiments demonstrating reaction to a small barrier of stones at meter 6 of the chute*

Numbers are snails recovered on 3 successive days; water flow was from left to right.

	Meters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	total
Hours	0	0	0	0	0	0	0	10	10	10	10	10	10	10	10	10	10	10	120
	24	0	0	0	0	0	0	40	48	8	5	5	4	3	2	0	2	3	0	120
	48	0	0	0	0	0	0	86	28	1	1	0	3	0	0	0	0	1	0	120
	72	0	2	0	0	0	0	110	2	3	0	1	1	0	0	0	0	1	0	120
Hours	0	0	0	0	0	0	0	10	10	10	10	10	10	10	10	10	10	10	10	120
	24	0	0	0	0	0	0	66	12	8	6	9	6	5	5	0	3	0	0	120
	48	0	0	0	0	0	0	92	6	5	3	3	5	4	0	1	1	0	0	120
	72	2	0	0	0	0	0	114	0	2	0	1	0	0	0	1	0	0	0	120

mental chute. During the six days of observations, only one marked snail was located below the release point. The recaptured snails were distributed throughout the dispersal area and the median animal as well as the more rapid moved in the upstream direction. On successive days the median snail was 0, 5, 10, 10, 15 and 15 meters upstream of the release-point (see Fig. 3).

Barrier experiments

A final experimental aspect of the problem was concerned with the simulation of the natural stream barrier under controlled conditions. This was done in duplicate experiments. Water in the upstream third of the previously described chute was impounded by a small obstruction of stones; this created a miniature pond, rapids, and flowing stream. Depth of the ponded water was 15 cm. and that of the flowing water 5 cm. with a 10 cm. drop.

In each of the 12 one-meter segments below the obstruction, 10 marked snails were dispersed uniformly. These were recaptured and their positions recorded at 24, 48, and 72 hours. The experiment was duplicated with a second set of 120 snails. As may be seen from the data of Table III, relation of the experimental population to the obstruction duplicated that found in the stream. Of the 120 released, 114 snails in one and 110 in the other of the two experiments were located in the meter-segment immediately below the barrier; in each experiment two snails had passed through or over the obstruction and were found in the upstream end of the ponded stretch. Some few either moved in both directions randomly, in the downstream direction, or not at all, as evidenced by their presence in a few of the downstream segments.

DISCUSSION

The aggregations of the snail *C. decisum* constitute atypical population densities for the stream studied. At two points, the upstream physical blocks of logs, rocks and gravel were concomitant with the aggregation. No comparable situations were found in a scrutinized half-mile stretch of stream. Increased densities were recorded for marginal areas high in organic content; this would appear to be a function of food availability (Allison 1942). These increased numbers did not constitute aggregations of the type described.

In seeking causes for the phenomenon it is unnecessary to infer a social behavior when it is readily explained by the

reaction pattern of individual animals to direct environmental action (Allee 1927, 1931). In this instance it is sufficient that the snails were orienting to physical gradients of current, gravity, or both, in a limited space, *i.e.*, blocking of upstream movements. No linear differences in the other physical or biotic factors were observed.

The upstream dispersal of *C. decisum* was demonstrated by released and recaptured snails under the natural stream conditions and under controlled experimental conditions in a confined chute. This reaction was noted in relatively swift waters and in a very slight current of the magnitude prevailing in pools of quiet waters found at intervals in streams of this type. This orientation to flowing stream waters comes as no surprise; the rheotactic response of stream animals has been studied and reported particularly in the early years of this century. Much of this is reviewed by Fraenkel and Gunn (1940) who note that this behavior occurs "in fact in practically all the active inhabitants of streams." The fact of upstream movement, rather than the equally interesting physiological mechanisms contributing to the behavior, is of importance to the problem.

In the presence of water movement and a very slight positive upstream inclination, the orientation and movement of experimental animals was positive. The experimental evidence indicates that the inclination of the substratum in the absence of current has no directional action on snail movements. Under natural conditions, pools of deeper water afford local differences in inclination under constant current conditions; the negative slopes of these pools did not hinder upstream movement. Gravitational gradient alone appears insufficient to stimulate this movement, but the combined effect with current is not eliminated as a possibility. Since the gradients of current and gravity are linked it may not be profitable to distinguish between them.

If the upstream movement of this species is characteristic, the presence of a block to such dispersal will effect a space limitation resulting in the piling up of individual snails into the aggregations observed. The effectiveness of the natural barriers was unequal; in one instance the stream had broken through and left a central gap below which the numbers of snails were smaller than below the other barrier which extended the width of the stream. Many micro-replicates of this situation were observed; any partially buried log maintained a small aggregation of snails on its lee side. It was of interest to find that Van Cleave and Altringer (1937) observed a similar situation. They say of *Campeloma rufum* in Illinois: "A small dam across the salt fork . . . helps maintain especially favorable conditions for molluscan life for several hundred yards downstream." Exceptionally large numbers were collected by them at this point, a situation noted previously by Baker (1922).

How does it happen that this species is relatively unable to traverse small barriers? In the stream, no snails were observed to be traversing the exposed surfaces of rocks. In the experimental chute with simulated rapids, this was also true. In three days, only 2 of 120 snails were able to pass the small block. The clue appears to be in the burrowing habit. In the stream and chute the animals accumulated in the gravel substratum below the block, unable to utilize the surface detour. It is probable that this feature of the animals' behavior accounts for its relative inability to negotiate rapids.

A datum peripheral to the problem was that of determination of the "snail's pace." A group of snails moving most rapidly within the chute aproximated 8 meters per day total dispersal distance. In the stream, speed of the same magnitude was observed over several days on the part of marked specimens. Barring setbacks by spring flood waters, which undoubtedly occur, *C. decisum* is able to rapidly populate a stream. This could occur after

chance introduction into an established stream, or by slowly pushing up tributaries with the developing drainage patterns over a long period of physiographic history.

It should be noted that the few individuals able to pass a barrier would have little difficulty repopulating the upstream stretch of the stream. *C. decisum* and the genus *Campeloma* generally appear to be almost exclusively parthenogenetic. In several localities large numbers have been collected without the presence of males (Baker 1928; Van Cleave and Altringer 1937; Mattox 1938).

An account by Allison (1942) of reactions of *Campeloma* sp. to fecal matter in stream traps reports findings contrary to those here reported. His evidence from 153 marked snails, of which 52 were recovered, indicated a random movement with relation to current. This discrepancy may be due to species differences or to conditions not analyzed in either of the investigations, such as orientation to food versus water movement.

Summary

1. Unusually high population density of the snail *Campeloma decisum* was noted at two points in a small Michigan stream.

2. The concomitance of these aggregations with the presence of rapids directly upstream prompted investigation of rheotactic response.

3. Under controlled and natural conditions, release-recapture experiments with marked snails indicated a positive upstream movement.

4. Experiments designed to simulate natural reactions to a physical barrier in flowing water resulted in duplications of the aggregation phenomenon observed in the stream.

5. It was concluded that the aggregations of snails noted could be related to the two responses: upstream dispersal and relative inability to traverse even a very slight block to the upstream movement, this inability perhaps being associated with the burrowing habit of this species.

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INFLUENCE OF POCKET GOPHERS ON VEGETATION OF SUBALPINE GRASSLAND IN CENTRAL UTAH

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Because the earth cast up by pocket gophers (*Thomomys talpoides moorei* Goldman) is often conspicuous in subalpine grassland, the ecologist wonders what the effect of gophers is upon development of soil and vegetation, the range manager wonders whether gophers compete for forage with livestock and game, and the watershed manager wonders how they influence infiltration and erosion. Some believe that pocket gophers reduce total productivity by eating some plants and by covering others with upcast earth, or that they change the composition of vegetation adversely, destroying perennials and encouraging annuals. Others suggest that pocket gophers may play an important role in mixing and aerating the soil, so that the net effect of their activities is an increase in vegetation and an improvement in composition.

There is very little in the literature to resolve these questions and differences of opinion. Reid and Moore (1951) have shown that heavy concentrations of pocket gophers in mountain meadows of eastern Oregon keep depleted ranges in poor condition indefinitely. This poor condition was induced originally, however, by overgrazing of livestock. A preliminary report from the subalpine zone of the Grand Mesa in Colorado (McGinnies 1947: 51–54) shows that changes in subalpine vegetation over a 6-year period were slight where gophers were present, as compared with range where they had been removed. The apparent contradiction in these reports may arise from differing degrees of initial depletion by overgrazing.

In studying soil disturbance by pocket gophers in the subalpine zone of the Wasatch Plateau, Ellison (1946) concluded that they are an important agent in the process of soil formation and normal geologic erosion in this subalpine grassland. He also concluded that the activities of the pocket gopher greatly increase accelerated erosion once this process had been set in motion through denudation of cover by excessive livestock grazing. However, few details were given about the effects of gophers on vegetation, an important phase of study which the present paper is intended to supply.

The subalpine zone of the Wasatch Plateau, lying mostly between elevations of 9,500 and 10,500 feet, is characterized in the main by rolling, gentle topography. The vegetation is herbaceous for the most part, particularly on level areas and on warm southerly and westerly slopes of moderate steepness. As a result of years of heavy grazing by domestic livestock, particularly sheep, this range is now dominated by rhizomatous species—chiefly *Artemisia discolor*[1] (sweetsage), *Penstemon rydbergii* (Rydberg penstemon), and *Achillea lanulosa* (western yarrow)—and by such aggressive seed-producers as *Stipa lettermani* (Letterman needlegrass) and *Taraxacum officinale* (dandelion). Steep southerly slopes are often partly or completely dominated by tall shrubs. On cool, steep northerly slopes are forests of Engelmann spruce and alpine fir. Small patches of spruce and fir also occur at

[1] Nomenclature of plant species follows that of Rydberg (1922), Tidestrom (1925), Kearney and Peebles (1942), and Kelsey and Dayton (1942).

intervals within the herbaceous type, forming a parkland. Pocket gophers confine themselves to herbaceous or brushy vegetal types; evidence of their activity is virtually never found in the timber. The only exception is in incompletely stocked young stands where the original timber has been destroyed by fire.

The soils of this part of the Wasatch Plateau are derived from shale and limestone, and are chiefly clays and clay loams. They are therefore heavy, and are very sticky when wet, but hard and unyielding when dry. The normal solum (true soil) of herbaceous types is 18 to 24 inches deep, and on some sites even deeper. Much erosion has occurred through loss of vegetal cover by overgrazing, and on some sites the soil has been stripped away to bedrock or a heavy erosion pavement.

Annual precipitation in the subalpine zone is about 32 inches (Lull and Ellison 1950). Beginning about November 1, the ground is covered by snow. The snow lies very deep during winter, and by spring, on the average, contains some 24 inches of water constituting approximately three-fourths of the annual precipitation. This is the source of yearlong stream flow. Most of the snow is usually gone about the last week in May, although drifts may persist most of the summer and in some years a few may last all summer long. Precipitation in summer is often erratic in distribution and may fall in violent storms. This high-intensity rainfall is readily absorbed into the soil where there is a dense cover of vegetation, whether this vegetation be herbs, brush, or trees. Where vegetal cover has been destroyed or greatly depleted, rainfall is less likely to soak in and may run over and erode the exposed ground surface (Forsling 1931).

In the subalpine zone the wind is usually blowing, and although temperatures are prevailingly low as compared with temperatures at lesser elevations, evaporation is rapid. In some summers several weeks may pass without rain. Active vegetal growth begins as the snow melts in spring, and, unless stimulated by fall rains, is completed toward the end of September. The growing season, then, may last about 4 months, but it may be shorter in some years because of cold weather in spring or fall, or because of drought.

The burrowing habits of the pocket gopher are closely correlated with the seasonal climatic cycle. The gopher is very active in winter, doing a great deal of digging, and traveling extensively on the surface of the ground by making tunnels through the snow. With the protection of the snow cover he is probably quite safe from predators. Part of the record of these activities in the snow is traced by the cores of earth with which the gopher plugs some of his snow tunnels, in this way disposing of much of the soil he excavates. In summer the excavated soil is pushed into surface piles at varying distances along the runways and in amounts ranging from a small handful to several quarts. Gopher activity is not particularly marked early in the summer; mounds become increasingly abundant toward late summer and in the fall. They tend to be formed most frequently during cloudy and rainy weather, and least frequently during dry spells.

The main runways of the pocket gopher burrows communicate with extensive feeding runs which parallel the ground surface at a depth from 3 to 6 inches, while the living quarters are usually somewhat deeper. Old runways are often plugged with fecal deposits or are filled with dirt removed in developing new tunnels. Practically all soil brought to the surface in summer has been newly excavated.

Because of the fossorial habit of pocket gophers, their food is largely procured underground. It includes fleshy taproots, tubers, and corms found while excavating their runways, and to a lesser extent green materials such as leaves and stems from the ground surface near the mouth of the burrow opening. Gophers do some feeding from the mouths of their burrows, their body length being the maximum radius of operation, and in this way they

also collect nesting materials (Aldous 1951).

Methods

The study site, which was as homogeneous as could be found, occupies 4 acres on a moderate westerly slope (9½ per cent) at about 10,000 feet elevation. This general area had been heavily grazed by livestock, mostly sheep, for about 70 years. In 1942 a rectangular area 391 × 448 feet was fenced against livestock. This fenced area lies with its long axis north and south on the contour. The plan has been to eliminate pocket gophers from one portion as completely as possible, leaving them undisturbed on the other. The distal thirds of the fenced plot were used as sampling areas, with the central third, half trapped and half untrapped, lying between as a buffer strip.

Pocket gophers

Before trapping in the late summer of 1942 a comparison of pocket gopher numbers was made on the two sides of the study area by counting fresh gopher mounds each day for a period of 5 days. The numbers of fresh mounds on the two halves were very nearly equal, indicating that gopher populations were about the same.

At the conclusion of the mound counts, gophers in the northern half were trapped out as completely as possible. The 1942 trapping was started the last two days of August and continued until no more animals could be taken. Beginning in 1943 and continuing through 1950, trapping was done in July and again in September. A considerable buffer area was also trapped outside the fence on three sides of the northern half in an effort to keep pocket gophers from migrating into the trapped study area.

There appear to be two ways in which pocket gophers reinvade the trapped area. Some may come in by way of snow tunnels, either from the outside or from the untrapped area. Others, so small at the time of trapping that they are not caught, may live to become established. In July 1948 a rodent-proof tin and small mesh fence was constructed across the middle of the central buffer strip. It was hoped that this fence would cut down the possibility of gophers getting into the trapped area from the untrapped side. During winter, when snow is deep and well over the top of the fence, it is possible that some gophers tunnel over. There has been no evidence that they get across by digging under the buried wire.

As a result of trapping in July and again in September very few gophers are left on the trapped area and the length of time they are there is restricted. A comparison of numbers of workings on the two halves at any time of year shows clearly that the difference in numbers of gophers is very great. For this reason the terms "gophers absent" and "gophers present" will be considered sufficiently accurate to contrast the trapped and untrapped areas.

Except for mice, other rodents on the trapped area were practically absent until about 1948 when groundsquirrels (*Citellus armatus* Kennicott) were first seen close by. Squirrels that come into the controlled area readily occupy vacant gopher tunnels. It is also believed that they are aggressive enough to take over occupied gopher runways. Poison has been set out to control squirrels each year when they first come out of hibernation and again during the course of gopher trapping operations. Surface poisoning for squirrels is believed to have little effect on pocket gophers because of the differences in their feeding habits.

Vegetation

The vegetation was first sampled in 1942 at the time the difference in treatment was imposed, and again in 1944 and 1950. Sampling was done by means of weight estimates (Pechanec and Pickford 1937) on permanent 1 × 3 m plots. These plots were so established as to grid the northern and southern thirds of the 4-acre area, leaving one-third of the area unsampled as a buffer strip between. There

were 41 1 × 3 m plots on the side where gophers were trapped and 36 on the side where they were undisturbed. These give a sampling intensity of approximately 2 per cent.

Considerable care has always been taken in training estimators, in order to insure reasonable accuracy. Estimate standards were frequently checked by estimating, clipping, and weighing samples. In addition, estimators have made a practice of alternating between plots under the two treatments, so that any tendency for a drift in standards would not influence the comparison. Herbage samples have been collected and dried at each examination so that the estimates could be reduced to an air-dry basis.

TABLE I. *Numbers of pocket gophers trapped from an area of 1.3 acres, 1942 to 1950*

Year	Adult	Immature	Total
1942	24	20	44
1943	6	21	27
1944	4	17	21
1945	8	7	15
1946	8	6	14
1947	3	16	19
1948	7	17	24
1949	6	10	16
1950	2	2	4
Total	68	116	184

RESULTS

In 1942 trapping accounted for 44 gophers on the 1⅓ acre controlled study area (Table I). This represents a popu-

TABLE II. *Air-dry herbage production (pounds per acre) in 1942 before treatment and in 1944 and 1950 after maintenance of pocket gophers on one experimental area and their suppression on another*

	Gophers present			Gophers absent		
	1942	1944	1950	1942	1944	1950
Taprooted Species:						
Agoseris pumila	10.41	17.49	22.62	8.63	11.97	14.09
Taraxacum officinale	289.30	241.13	24.45	65.03	97.88	94.39
Others	4.68	5.94	2.78	4.79	8.43	19.90
Subtotal	304.39	264.56	49.85	78.45	118.28	128.38
Rhizomatous Species:						
Achillea lanulosa	130.77	140.67	76.65	76.63	110.11	83.65
Artemisia discolor	167.25	150.18	309.99	335.55	204.14	166.94
Aster chilensis	8.51	14.57	24.88	2.94	3.63	10.62
Erigeron ursinus	1.90	4.59	4.86	0.60	1.00	2.69
Penstemon rydbergii	299.68	266.73	353.64	148.97	154.50	135.07
Solidago ciliosa	5.43	10.94	24.41	2.82	2.65	3.99
Vicia americana	5.05	13.14	47.99	15.38	28.95	37.40
Subtotal	618.59	600.82	842.42	582.89	504.98	440.36
Grasses and Sedges:						
Agropyron trachycaulum	26.09	39.56	51.61	13.97	34.78	10.89
Stipa columbiana	6.02	13.64	21.01	6.76	11.78	6.15
Stipa lettermani	69.13	58.89	52.95	229.50	241.06	231.83
Others	9.71	11.84	16.41	3.29	4.99	1.82
Subtotal	110.95	123.93	141.98	253.52	292.61	250.69
Tall Forbs:	35.88	40.46	47.25	27.66	37.14	40.00
Ephemerals	25.09	24.12	13.31	48.89	33.08	22.72
Annuals	22.75	18.95	8.05	8.89	6.12	0.00
Shrubs (*Chrysothamnus viscidiflorus* only)	—	—	—	0.28	2.26	0.96
Total	1,117.65	1,072.84	1,102.86	1,000.58	994.47	883.11

lation of 33 gophers of all ages per acre. Of the 44 gophers trapped, 24 were classed as adults and 20 as immature. In fetal examination of 39 pregnant females 126 embryos have been found, or an average of 3.23 per female. This would indicate that the number of immature gophers should exceed the number of adults. Since adult animals outnumbered juveniles in 1942, it may be that some dispersion of the young had already taken place by the time trapping was done.

The effects of trapping are reflected in the reduction in number of adult gophers after 1942. Most gophers trapped in subsequent years were juveniles, indicating that influx of young was the chief cause of fluctuation in total numbers. These figures show that consistent trapping is necessary, even with a trapped buffer strip around the experimental area, to keep the gopher population at a low level.

In the course of this study only the females trapped in July have contained unborn young, strongly indicating that only one litter is produced at this elevation by any female in any year.

Of the total 68 adult animals listed in Table I, 37, or 54.4 per cent, were males; of the 116 immature animals, 62, or 53.4 per cent, were males. It thus appears that there is a slight excess of males over females.

Total production of vegetation under the two treatments has not changed greatly over the 8-year period (Table II). In examining the two areas in the field, one has to look closely to detect differences in vegetation, and the discernible differences are so slight that one is doubtful, from inspection alone, whether to attribute them to treatment or to inherent variability (Fig. 1). The totals in Table II show a slight downward trend on both sides, more marked where gophers have been removed than where they have been

FIG. 1. View eastward along rodent-proof fence separating the portion of the study area from which pocket gophers have been trapped (left) from portion in which they have been undisturbed. Most of the area in view here is the central buffer strip. After almost 9 years of treatment marked differences in appearance of the vegetation are not apparent. July 20, 1951.

undisturbed. It cannot be said, therefore, that pocket gophers have reduced total production; relatively, they may have increased production slightly.

Perhaps the reason that differences are not more apparent to the eye is that the vegetation itself is naturally variable. Table II illustrates this point. In 1942 before the treatment was imposed, Letterman needlegrass was over three times as abundant on the side from which gophers were to be removed as on the other side. At the same time dandelion was more than four times as abundant on the side where gophers were to be undisturbed as it was where they were to be removed. This natural variability is believed to be unavoidable; it occurred in spite of careful selection of the study area for homogeneity. In our opinion, the likelihood of finding any more uniform area of 4 acres in this subalpine grassland is slight.

One change that has taken place is the strong decline in dandelion where gophers have been present. Here, in 1950, there was less than 10 per cent of the dandelion that was present in 1942. On the area where gophers have been removed, in contrast, it increased about 50 per cent during the first 2 years of trapping and maintained itself at about the same level for the last 6 years. Dandelion is one of the favorite food plants of pocket gophers. Numerous caches have been found in which the dried taproots of this species were the principal item stored (Aldous 1945), and new runways are sometimes marked on the surface by the withered tops from which the roots have been severed. It is probable, therefore, that foraging by pocket gophers has reduced the dandelion.

Pocket gophers had access to the "gophers present" area before the land was fenced. If the population of gophers had not changed, one might suppose the volume of dandelion would have remained about the same. The very strong decline in dandelion that has occurred therefore suggests that the population of gophers here has increased during the 8-year period. The relative amounts of surficial disturbance today inside the "gophers present" area and on the untrapped open range to the south support this belief, and it is in accord with many observations that pocket gophers tend to concentrate in livestock exclosures.

It is interesting to note that the native *Agoseris* (mountain dandelion), which is much like the introduced dandelion in growth-form, and which presumably would also be a good pocket gopher food, has behaved very differently. Mountain dandelion occurred in approximately equal amounts on both sides in 1942. It has increased even more where pocket gophers were present than where they were absent. Despite apparances, therefore, it may not be much eaten by gophers.

Other taprooted perennials, particularly *Lesquerella utahensis* (bladderpod), *Arabis lyallii* (Lyall rockcress), *Pseudocymopterus montanus,* and *Thlaspi glaucum* (blue pennycress), have increased rather markedly where gophers have been absent, but have increased less markedly, or have decreased, where gophers have been present. The amounts involved are so small that it does not seem safe to attribute these changes to the influence of gophers, even though they are generally similar to the changes in dandelion. Taprooted species that have occurred sporadically and in such small amounts that no trends can be inferred are *Frasera speciosa* (elkweed), *Rumex mexicanus* (Mexican dock), and *Plantago purshii* (woolly Indian-wheat).

Among rhizomatous species, which make up more than half the total vegetation (but with the exception of yarrow), there is a tendency for rather marked increases with pocket gophers present. The change in sweetsage is particularly notable. Over the 8-year period this herbaceous sage declined strongly where gophers were absent and increased strongly where they were present. This change in sweetsage has been the major influence affecting the subtotals for the rhizomatous species, and it is more than enough by itself to account for the 117-pound decline in total

FIG. 2. Vigorous growth, at left, of rhizomatous sweetsage (light) and penstemon (capitate inflorescence) around edge of groundsquirrel disturbance, in contrast to their reduced growth at right on an undisturbed surface.

production between 1942 and 1950 on the side where pocket gophers are absent. It is quite clear in the field that sweetsage production is augmented where this plant can vegetatively invade bare areas formed by gopher diggings. Possibly there are no more shoots per unit of area, but many of the shoots that are present are distinctively tall and robust. In contrast, where there are few or no bare areas and sweetsage must compete on equal terms with the other species with which it is intermingled, it grows much less vigorously (Fig. 2).

Among the other rhizomatous species, penstemon shows the same net trend as sweetsage—an increase where gophers are present and a decrease where they are absent. The other rhizomatous species—*Aster, Erigeron* (wild-daisy), *Solidago* (goldenrod), and *Vicia* (vetch)—have increased on both sides, but in each case more markedly where gophers are present than where they are absent. Perhaps the explanation that has been given for the spread of sweetsage is also applicable to these other five rhizomatous species. *Poa pratensis* (Kentucky bluegrass), the only rhizomatous grass, and a very minor species, has declined on both sides, but more markedly where gophers are absent than where they are present.

The one rhizomatous forb that does not respond like the others is yarrow: its fluctuations seem to bear no relation to the activities of pocket gophers.

Grasses and sedges have changed relatively little where pocket gophers are absent, but they have increased markedly—particularly *Agropyron* (wheatgrass) and *Stipa columbiana* (subalpine needlegrass)—where gophers are present. It would appear from this that pocket gophers are not harmful to native grasses. "Others" in Table II include *Bromus carinatus* (mountain brome), *Carex festivella* (sedge), *Hordeum nodosum* (meadow barley), *Poa pratensis,* and *Trisetum spicatum* (spike trisetum). Most of the net increase in "Others" where gophers are present is attributable to an increase in *Bromus,* which is present on the infested side of the plot but not on the other.

Tall forbs, which are infrequent in occurence as yet, have increased slightly on both areas. The species that have increased include, in order of abundance, *Thalictrum fendleri* (meadowrue), *Potentilla pulcherrima* (beauty cinquefoil), *Geranium richardsonii, Ligusticum porteri* (loveroot), and *Polemonium foliosissimum* (blue skunkleaf). *Erigeron speciosus* (Oregon wild-daisy), *Potentilla glandulosa* (gland cinquefoil), and *Silene lyallii* have decreased. A general increase in tall forbs is usually noted on subalpine range after sheep have been excluded for several years, and as time goes on Oregon

wild-daisy may be expected to become especially abundant on this range. There is no difference in the changes of these tall forbs that is clear-cut enough to be ascribed to pocket gophers.

In approximate order of abundance, species classed as ephemerals (*i.e.*, early withering perennials) and annuals are as follows:

Ephemerals

Viola nuttallii linguaefolia (tongueleaf violet)
Ranunculus inamoenus (buttercup)
Delphinium menziesii (spring larkspur)
Stellaria jamesiana (chickweed)
Erythronium grandiflorum (trout lily)

Annuals

Collomialinearis
Polygonum douglasii (Douglas knotweed)
Androsace septentrionalis (biennial) (rock jasmine)
Chenopodium album (lambsquarters)
Descurainia incisa (biennial) (western tansymustard)
Orthocarpus tolmiei (owl clover)
Lepidium sp. (pepper weed)
Draba sp.
Gentiana sp.

These species have declined strongly on both areas. Annuals have declined more slowly where gophers have been undisturbed than where they have been removed, and at times they have been especially conspicuous on the bare soil of old gopher mounds. It appears, therefore, that annuals are encouraged to some extent by pocket gophers. However, the great decline of ephemerals and annuals, like the increase of tall forbs, probably relates more to elimination of livestock grazing than to influence of pocket gophers.

It has been evident for several years that the soil of the south side of the experimental area, where gophers are present, is much looser and softer than the soil of the north side where gophers are absent. One is aware of the difference as he walks from one end to the other: his shoes settle into the ground on the south side, but on the north side he walks on a relatively hard surface. The difference is even more marked between the south side and the adjacent grazed range where gophers are also present. The difference may be attributed both to a greater number of gophers inside the fence, and to the trampling of the outside soil by livestock, for one can feel a somewhat similar difference along the north side where gophers are practically eliminated both inside and out. A number of people who have walked across the area, but who have been unfamiliar with the details of this study, have corroborated these observations on tilth of the soil.

It is possible that this difference in feel of the soil and in production of vegetation reflects a north-south gradient in soil depth or soil quality, but we think not; the changes are fairly abrupt at the fence lines. Unfortunately, without replication of treatment the facts cannot be better established at this time. If the effects of pocket gophers on tilth of the soil and on productivity are real, a continuation of the study (which is intended) should produce more marked differences.

If these observations are correct, it appears as if pocket gophers, through cultivating and aerating this very heavy soil, perform a distinctly useful function. This activity probably increases the over-all infiltration capacity of the soil, even though small bare spots from gopher workings are scattered throughout the stand. Such activity is probably especially needed in heavy soils that are trampled by livestock. Furthermore, although pocket gophers may compete with livestock for certain pre-

ferred forage plants (a question on which this study bears only partly), they do not decrease total production, but probably increase it, over and above the forage they consume.

Summary and Conclusions

Half of a 4-acre fenced plot in the subalpine zone of the Wasatch Plateau has been systematically trapped since 1942 to free it from pocket gophers. Pocket gophers in the other half have not been disturbed. Weight of vegetation has been estimated three times: in 1942 before the effects of trapping could be felt, in 1944, and in 1950.

At the initial trapping in the late summer of 1942 the gopher population was estimated to be 33 per acre, although some young may have dispersed by that time. Subsequent trapping twice yearly has reduced the adult gopher population from 24 on the 1.3-acre study area to a level between 2 and 8. Most of the gophers caught exert an influence on the "gophers absent" side only part of the year. It is believed that the gopher population on the "gophers present" side has increased since 1942.

Results of trapping indicate that an average of 3.23 young are produced per pregnant female, that no more than one litter is produced per female per year, and that there is a slight excess of males over females.

Total production of vegetation (roughly half a ton of air-dry matter per acre) has not been greatly changed in 8 years of treatment. There is a slight tendency for total production to increase where gophers are present as compared with where they are absent.

Common dandelion has decreased strongly where gophers are present and has increased where they are absent. This difference is attributed to foraging by gophers. Mountain dandelion, however, which also has fleshy taproots that might be supposed equally suitable as food, has not responded in the same way.

Rhizomatous species, with the exception of yarrow, have increased where gophers are present as compared with their behavior on the area from which gophers have been removed. This is particularly true of sweetsage. Evidently species with established underground parts are able to take over bare areas and to grow especially vigorously where other vegetation has been removed by gophers in disturbing the soil.

Grasses and sedges tend to increase where gophers are present as compared with where they are absent.

Most tall forbs have increased on both sides of the experimental area, and annuals and ephemerals have declined. These trends are probably the result of exclusion of livestock.

Where pocket gophers are present the soil is distinctly softer and looser than where they have been removed. It appears probable that gophers perform a useful function in loosening the soil, a function which seems particularly important in heavy clay soils subject to compaction under livestock grazing.

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THE RELATION OF INSECTS AND INSECT-BORNE DISEASES TO THE VEGETATION AND ENVIRONMENT IN LIBERIA [1]

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Introduction

The object of this work is to draw attention to a field which has not been explored ecologically on a wide scale in the West African Republic of Liberia—a field in which the writer became interested during his stay in that country from 1943 to 1945 while serving as Commanding Officer of the 16th Malaria Survey Detachment, Army of the United States. Much of the biological research in Liberia up to that time had been systematic. It is, therefore, not surprising that emphasis in the scientific literature pertaining to Liberia is taxonomic and distributional.

This study has as its major points of emphasis various phases of the ecology of insects and insect-borne diseases. An attempt has been made to show the interrelations between the insect vectors of parasites of man and vegetation. The relations between soil, vegetation and climate were studied in order to gain a clearer understanding of the pattern of distribution of the vegetation and therefore of the insects associated with the plant communities. The geology was studied in order to get a better understanding of the soils.

When it is remembered that a very large part of the practice of medicine is dealing with diseases caused by animal parasites, the great importance of ecological studies in the control of such diseases is obvious.

I wish to thank C. F. W. Musebeck and staff of the Bureau of Entomology and Plant Quarantine for aid in determining the insects. I am also grateful to Joseph C. Bequaert, Curator of Insects, Museum of Comparative Zoology, Harvard University, for revising the Tabanidae and Vespidae and for determining the mollusks. Finally I am greatly indebted to Edward G. Reinhard, Hugh T. O'Neill and Herbert C. Hanson of the Department of Biology, the Catholic University of America, for various kinds of assistance. Part of this paper was used in the dissertation, "Some Ecological Aspects of Liberia as Interpreted from the Vegetation on Ground and Aerial Photography with special reference to the Distribution of Parasites," which was submitted in partial fulfillment for the Ph.D. degree received from The Catholic University of America in June 1950. Acknowledgment is due Dr. Hanson for assistance in the preparation of this manuscript.

Review of the Literature

Medical and economic aspects of insects and other arthropods were studied by Strong and others (1930). Barber, Rice, and Brown (1932) found a high incidence of malaria among native laborers on the Firestone Rubber Plantations and sufficient gametocyte carriers to insure the production of large numbers of sporozoite-infected anopheline mosquitoes. Edwards, in a systematic paper (1941), described many of the adult culicine mosquitoes and their pupae. Moore (1945) discussed, from a medical point of view, the malaria incidence among American troops shortly after their arrival in Liberia. In 1946 Bequaert reported the results of his study on the distribution, ecology and control of tsetse-flies. Briscoe (1947) recorded the distribution of 128 determined and 76 undetermined species of insects. Attention was drawn to the anti-*gambiae* program at the U. S. Army installations by Farrell

[1] A contribution from the Department of Biology, The Catholic University of America, Washington, D. C.

(1948). Poindexter (1949) reported the results of a clinical survey of the major infectious diseases from five sections of Liberia, and, in 1950, called attention to the uneven distribution of *Wuchereria bancrofti.* The ecology and distribution of mosquitoes are discussed in a paper by Briscoe (1950*a*). An attempt was made by the same writer, in his dissertation referred to above, to connect the studies on parasitology and insect vectors with the type of vegetation in Liberia, especially the recognition of such vegetation on aerial and ground photography. Briscoe (1950*b*) also reported a brief account of Bancroft's filariasis in the Central Province of Liberia and has in press (U. S. Department of State) an annotated bibliography with approximately 240 titles pertaining to the scientific literature on Liberia.

Bentham and Hooker (1849) included an account of 150 species of plants collected by Theodor Vogel in their *Flora nigritiana.* (The botanical explorations of Liberia began with the arrival of Vogel at Monrovia on July 5th, 1841.) Plants collected in Liberia by Phillip Schoenlein were mentioned by Klotzsch (1856). Engler (1889) incorporated in his work the plants that were collected in the marshes near Monrovia by Nauman. Stapf (1905) wrote a systematic account of the Liberian flora in Latin and Johnston (1906) brought together, as far as possible, all the information known about the flora. Engler and Drude (1910) briefly described a mangrove community. There is a discussion of the forests and forest products by Korn (1926). Keys to genera and species, and brief notes on the distribution of plants are incorporated in the monumental work of Hutchinson and Dalziel (1927, 1931). In 1930 Thériot published an annotated list of mosses that were collected by H. D. Linder. Descriptions of the types of Liberian forests with notes on their commercial importance were reported by Cooper and Record (1931). Bouet (1932) discussed the progress made in Liberia in the development of the Brazilian rubber trees, *Hevea brasiliensis,* and Dinklage (1937) added a list of vascular plants collected during his botanical explorations. Agriculture in its broadest sense was treated by Warner (1945). Baldwin and Speese (1949) found thousands of flowering plants of *Emilia sagitta* growing among marsh vegetation in the Eastern Province of Liberia but only three small populations of *E. sonchifolia.* The same authors (1950) reported *Aeglopsis chevalieri* from the hinterland; only a single tree, however, was found. Baldwin (1950) gave distributional notes for *Maschalocephalus dinklagei* and indicated on a map the localities where the collections were made.

Methods

Most of the data for this study were obtained by direct field observations. The insects, excepting the mosquitoes, were collected in sweeping nets. A number of insects could always be collected by hand beneath stones and decaying wood and in termitaria. The collected specimens were immediately placed in killing jars containing cyanide. When cyanide jars were not available the writer used ether bottles.

Adult mosquitoes were collected with an aspirator both indoors and outdoors. Larvae and pupae were collected with dippers or pipettes.

Detailed studies were made of the various plant communities such as outer strand vegetation, mangrove, Pandanus-Raphia community, savannas, rain forest, and gallery forest (fringing forest). These plant studies were augmented by (1) airplane flights over the country, (2) aerial photography made by the Abrams Aerial Survey 1936–1937, and (3) the collection of Liberian plants in the U. S. National Herbarium.

Regional Geography

The West African Republic of Liberia, approximately 43,000 square miles in area, lies on the Guinea Coast of Africa

FIG. 1. MAP OF LIBERIA

between the British colony of Sierra Leone on the west and the French colony of the Ivory Coast on the east. The coastline, all on the Atlantic Ocean, is a low-lying sand beach about 350 miles long. Lagoons, tidal creeks, and the estuaries of rivers indent the coastline in several places but nowhere form good natural harbors. (See map, Fig. 1.)

The lagoons lie parallel to the ocean and are separated from it by sand bars. Many small creeks empty into them. During the rainy season there is considerable flow from these lagoons into the ocean. By far the largest lagoon is Fisherman's Lake. It is 10 miles long and 3 miles wide and is under the influence of the tides. This brackish sheet of water is fringed with mangrove trees on the landward side. Many estuaries enter the lagoons which are connected with the ocean through the mouths of the rivers.

One of the most notable features of the coastal region is its three promontories. The most striking promontory is Cape Mount. It is situated near the western boundary and has an elevation of more than 1000 feet. The city of Monrovia is built on the northwestern end of Cape Mesurado. This promontory is 260 feet above sea level. Cape Palmas, the third promontory, is near the southern boundary of the country. It has an elevation of 104 feet.

Climate

Liberia has one of the most humid and rainy climates of Africa. The rainfall is

seasonal and is directly related to the shift of the sun and the latitudinal migration of the wind belts. Maximum precipitation occurs at the time of the high-sun period (May to October). At the time of low sun (November to April) the subtropical high pressure belts migrate southward and the northeast trade winds that blow across the country are dry.

The center of maximum precipitation is situated along the coastline where the total amount may be as much as 170 inches. The period from May to October is known as the "wet" season. However, the so-called "dry" season, which extends from November to April, has no month without some rain.

The rainfall is heavier than in most other parts of Africa with the exception of the Cameroons. At Harbel Plantation in the Central Province, for instance, the average total rainfall for the twelve-year period 1928–1940 was 145.62 inches (Strong and others 1930) and was distributed as follows:

J	F	M	A	M	J	J	A	S	O	N	D
1.26	1.94	5.22	5.73	13.41	21.00	19.15	23.30	28.03	15.94	7.31	3.33

It rains throughout the year in the coastal region in Liberia. Most of the rain falls during the "wet" period (May to October). At Roberts Field in the Central Province the average total annual rainfall for the three-year period 1943–1945 was 146.28 inches (maximum 170.40 inches in 1944; minimum 123.20 inches in 1945). The wettest months are usually July and August. However, in 1943 they were August with 27.90 inches and September with 31.94 inches, while in 1944, June with 53.72 inches was the rainiest month. January and February are usually the two driest months. In 1945 they had 1.70 inches and 0.40 inch of rain respectively. The average monthly rainfall for the three-year period 1943–1945 was as follows:

	J	F	M	A	M	J	J	A	S	O	N	D	Total
1943	0.16	4.88	5.56	7.42	10.88	22.09	8.53	27.90	31.94	13.97	5.94	5.84	145.25
1944	4.22	0.07	4.72	3.67	5.73	29.70	53.72	18.58	29.57	10.97	6.59	2.86	170.40
1945	1.70	0.40	3.10	6.03	6.96	20.45	29.58	11.58	20.40	16.00	6.00	1.00	123.20

The small amount of rainfall in March is associated with storms that occur near the end of this month. These winds and rains generally increase in frequency about the first week in April. At this time of year the parched soil absorbs the water very quickly. About the first week in May showers come several times a week; heavy rains begin the latter part of the same month. Torrential rains are almost continuous for 5 or 6 days and nights. This may be followed by 4 or 5 days of relatively clear weather. During the months of July and August there is a short dry period which the Liberians call the "middle-dries." It generally begins about the last week in July and continues for a week or more. In September it rains almost every day. The rains tend to decrease in October until the middle of December when they occur as infrequent showers.

A sharp break in the rainfall is noted as one approaches the hinterland and the French Guinea boundary. Here the annual precipitation diminishes and the "dry" season is more pronounced. Though the pattern of the monthly distribution is similar to that along the coast, the total annual rainfall is just about a third as much.

The sensible temperatures of the Liberian littoral were never as oppressive as those in the District of Columbia, U. S. A., in July and August. Except in places like Monrovia where rock formation reflects the heat, the sensible temperatures in Liberia were not high. The persistence of the heat, however, is the factor that makes it more oppressive than is the case in the more temperate regions (Table I).

From July to September natives complain about the weather being cold. It is

TABLE I. *Monthly temperatures, ° F. Roberts Field*

Month	Maximum		Minimum		Average	
	1943	1944	1943	1944	1943	1944
Jan.	88	88	69	70	79	79
Feb.	89	92	72	71	80	81
Mar.	90	91	72	71	81	81
Apr.	90	92	72	72	81	82
May	87	92	73	72	80	82
June	85	87	72	71	78	79
July	80	82	70	71	75	76
Aug.	80	80	70	72	75	76
Sept.	89	83	71	72	80	77
Oct.	89	87	69	73	79	80
Nov.	89	89	70	72	80	80
Dec.	89	86	70	72	79	79

during this period that the daily minimum in temperature may be as low as 55° before dawn. Early December mornings are usually cool. The days are quite hot from October to December but the nights are always cool. During the "dry" period it is necessary to sleep under one blanket at night; two are necessary during the rainy season. Frequently when the midday temperature was 92° F. the humidity would decrease to such an extent that the cooling effect due to evaporation of moisture from the body would be quite pronounced. A hot and humid period of calm generally prevailed between 7 and 9 A.M. Quite often this was the most unpleasant part of the day. The total effect of insolation was felt from 11 A.M. to 2 P.M. It is during this time that one should refrain from vigorous activity. At 8 P.M. it becomes cool again.

Physiography

There is no coastal plain in Liberia; the rocks rise up from the shoreline. Krenkel (1925) states that the "rocks near the shore and some distance back are of the oldest sedimentary pre-paleozoic metamorphosed into schists and similar kinds, but farther back the very ancient igneous rocks, such as granites and their metamorphosed form gneiss, prevail at the surface."

Ancient schists, gneisses and gneissic granites are the oldest rocks in Liberia into which granites have intruded. Volcanic rocks occur near the coast and diabase outcrops were found along trails. Monrovia is built on a ridge of diabase. The diabases are relatively recent intrusions into schists.

A highly quartzitic phase of gneiss is the dominant type of metamorphic rock near the coast. It weathers to rather poor, sandy soil which is sometimes mistaken for beach sand because of the high silica content. The quartzitic rocks are quite resistant to erosion as compared to the granitic rocks which weather more readily. The most abundant igneous rocks are gneissic granites. They occur near the coast in the region of the Kpandemai Mountain. Except for alluvial deposits, only a small part of the surface of Liberia is unmetamorphosed sedimentary rocks (according to W. H. Newhouse and others in an unpublished manuscript on file at the U. S. Geological Survey).

The relief in Liberia shows a total range of 5,750 feet. To illustrate the increasing altitude from the coastal region to the interior, it may be stated that at Roberts Field the altitude is about 36 feet; at the town of Boporo, 340 feet. The altitude at the village of Zienzu is 505 feet while the maximum altitude of the Nimba Mountains is 4,200 feet. Near the French Guinea border, beyond the Nimba Mountains, the altitude increases to 5,750 feet.

A portion of the western boundary is formed by the Mano River which reaches the sea near Cape Mount after flowing through a region of dense forest. From the mouth of this river the trend of the coastline is in a southeasterly direction. Roberts Field, the site of the new airport, is in the drainage of the Farmington and Du Rivers. These rivers terminate in a common mouth at the little settlement of Marshall. The entrance of this estuary from the ocean has a very dangerous sand bar. The St. Paul River separates the Western from the Central Province. This is the second longest river in Liberia (about 200 miles long) and an important

communication link between Monrovia and trading posts in the hinterland as far as White Plains. Beyond this point, however, it is impossible to go further in native canoes because the river is considerably choked with vegetation. The St. Paul empties into the ocean about 4 miles northeast of Monrovia. The next important river is the St. John. After draining a large area of rain forest it enters the Atlantic near the village of Grand Bassa. Southward the Cess River, which also drains a portion of the rain forest, empties into the ocean near Nana Kru; next comes the Sanguin River, near Baffu Point. It is the Sanguin River which divides the counties of Sino and Grand Bassa. The Cavalla River, the longest river draining any part of Liberia, forms the southeastern boundary with the Ivory Coast. (See Fig. 1.)

The rivers flow from north to south in steep channels which are several feet below the general surface level, their exposed banks consisting of deeply weathered rock. As the rivers approach the coastline hard bedrock is encountered on the surface and rapids are formed. Despite the rapidly descending gradients of the larger rivers and the well-developed drainage pattern, there are many swamps in the hinterland. During the rainy season lowlying areas of jungle are flooded and a number of anastomosing streams are established.

Soils

According to William Reid, in an unpublished manuscript on file at the U. S. State Department, seven types of soil groups are recognized in Liberia. They are: humic latosol, bog, half-bog, gray hydromorphic, alluvial, lithosol, and sand.

Humic latosol. Approximately 75 per cent of the country consists of humic latosols. They occur on gently rolling land up to an elevation of 1800 feet. These soils vary in texture from coarse sand to clay but are mostly a mixture called sandy clay loam. Permeability and internal drainage are usually good. The crumb structure of the subsoil is a desirable condition as it enhances rapid internal drainage. The surface layer of soil to a depth of three inches is strongly acid, averaging about pH 4.5. These humic latosols are lateritic and supported the original tropical high forest including the rain forest type. Where the forest has been cleared by fire for farming these soils have more phosphorus but less organic matter than those areas that still support the primeval forest and have not been subjected to burning. After abandonment by the farmers secondary growth of low trees arises. Although humic latosols are quite deficient in plant nutrients they are the most productive soils in Liberia. Cultivated crops are produced successfully on gently sloping land by the application of fertilizers and green manure.

Bog soils. Underlying the coastal marshland, consisting of mangrove and a few herbaceous species, are bog soils. These marshlands are located on tidal lowlands near the mouths of rivers and in lagoons and shallow areas along the coast. They occupy 0.8 per cent of the country. These soils are peaty to mucky materials overlying bluish-gray clay or sand.

Half-bog soils. In a few scattered areas, more or less permanently saturated, where ferns, sedges and grasses form the major kinds of vegetation, dark-brown to grayish-black peaty or mucky loam soils are found overlying grayish sand or clay. They occupy about 0.4 per cent of the total area of the country. The acidity of the surface soil is about pH 4.6.

Gray hydromorphic soils. These soils occur in seasonally swampy land in valley floors and the vegetation consists of low trees, shrubby palms, grasses and sedges. These soils are found in small narrow areas and comprise about 25 per cent of the total area. They are quite different from the boggy soils above consisting usually of gray-brown or gray-black sandy loam over grayish-yellow subsoil. The pH of the top soil is about 4.6. If drained and fertilized they can be used for the production of rice.

Alluvial soils. These soils are found in strips along the rivers and stream beds and represent about 2.1 per cent of the country. The vegetation is forest or a mixture of forest and coarse grasses. The top soil varies from a sandy loam overlying reddish to yellowish-brown subsoil. The acidity of the surface three inches of soil averages between pH 4.2 and 4.7. These are the most productive for the growth of annual food crops.

Lithosols. These soils are formed on hilly and rough land occupying 16.7 per cent of the country. They are usually shallow and outcrops of rock occur. Vegetation is composed of shrubs and trees. The topsoil is dark-brown and varies in texture from sand to clay. The acidity in the surface three-inch layer is about pH 4.4. The relief and shallowness make the soils of most value for wild life and forest reserves.

Sands. The sands are found mostly in the narrow coastal belt inland from the coastal bog soils and in a few small areas farther inland. Vegetation is made up of a sparse stand of palms scattered in grassland. The soils are infertile but can be made productive by heavy applications of fertilizers. The cocoanut and oil palm appear best adapted; the wild date palms occur throughout the coastal strip.

As you fly from the ocean inland into Liberia the mangrove coastal marshland with bog soils is crossed first and then a narrow sand strip occupied by wild date palms is crossed before flying over the tall forest.

Within the country the various vegetation types and underlying soils can be recognized because the major proportion, 75 per cent, is occupied by tall forest with large clearings on latosol. Intermingled in the tall forest are a few scattered marshy areas with half-bog types of soils, shrubby palms, grasses and sedges in the floor of the valleys, and alluvial soils with forests and grasses along streams and river beds. Northward toward the French Guinea border the elevation increases and the relief becomes more rugged with the trees becoming scattered, shorter, and more scrubby. Shrubs also become numerous. The soils are shallow lithosols.

Vegetation

Many kinds of insects are closely associated with plant communities (Table II). The partiality of some of them (*e.g.* tsetse-flies) to certain kinds of plant communities is marked. Moreau (1935) has shown the relationship of birds to vegetation in East Africa.

There are six main vegetation types in Liberia: (1) outer strand or beach communities bordering the ocean; (2) mangrove forest which is inland from the beach and is subjected to daily tidal invasion; (3) Pandanus-Raphia communities growing in dense stands just above the tide level inland from the preceding; (4) savanna (trees or shrubs scattered in the grassland) that occurs in a narrow strip along the coast and the Mano River and in an irregular belt near the French Guinea border; (5) tropical rain forest characterized by a close grouping of trees as much as 150 feet high and occupying most of the country; (6) the gallery forest (fringing forest) extending northward from the rain forest along the banks of rivers. These vegetation types have been discussed in more or less detail in various parts of tropical Africa by several writers, especially Shantz and Marbut (1923), Ainslie (1926), Hutchinson and Dalziel (1927, 1931), Moreau (1935), Michelmore (1939), Edwards (1940), Burtt (1942), Warner (1945), Gillman (1949), and Gilliland (1950). Good (1947) classified the vegetation in Liberia and French Guinea into two floristic regions, *viz.*, the Sudanese park steppe and the West African forest.

Outer strand communities

The outer strand communities grow on the coastal sands (Warner 1945). The most conspicuous plant in this belt is *Phoenix reclinata* Jacq., a false date palm about 5 feet high, which, except at the estuaries, extends throughout the entire Liberian littoral from Cape Mount to Cape Palmas. This palm forms a long hedge-

like row which is very difficult to penetrate without the aid of a heavy sharp blade. Growing in this belt along with *P. reclinata* are extensive patches of *Sansevieria liberica* Ger. & Labr. Between the line of false date palms and the line of high tide are such common widespread strand plants as: *Ipomoea pes-caprae* L., forming slender vines at right angles to the coast; *Remirea maritima* Aubl., a small scrubby sedge about 1 foot high; *Cyperus ligularis* L., a sedge with stems 3 feet in height; and *C. maritimus* Poir, a rather stout sedge. Farther inland from the *P. reclinata* zone on the almost level sandy plains are *Dodonea viscosa* L., a viscid shrub about 4 feet high, and *Hibiscus surattensis* L., a trailing shrub growing along with *D. viscosa*. Also common in this region are *Napoleona vogelii* Hook & Planch., a shrub about 20 feet in height, *Heisteria parvifolia* Smith, a glabrous shrub about 20 feet high, and *Eriosema glomeratum* Hook, an erect, low-branching shrub.

Insects found in this habitat are: flesh flies, *Sarcophaga* sp., snipe flies, *Suragina* sp., shore flies, *Paralimna* sp., wasps, *Bembix* sp., *Belonogaster junceus, Rygchium marginellum, Synagris cornuta,* and bees, *Gronoceras praetexta* (Table II).

Mollusk shells collected in these coastal sands are: *Nerita glabrata* Sowerby, *Pachymelania aurita* Müller, *Zonaria zonaria* Gmelin, *Cypraea stercoralis* L., *Agaronia acuminata* Lamarck, *Thais nodosa* L., *T. haemastoma forbesi* Dunker, *T. coronata* Lamarck, *Siphonaria pectinata* L., *Fissurella nubecula* L., *Terebra cuspidata* Hinds, *Natica marochiensis* Gmelin, *Clanculus costatum* L., *C. ringens* Brug., *Senilia senilis* L., *Arca imbricata* Brug., *Dosinia lupinus afra* Gmelin, *Mactra nitida* Spengler, *Diplodonta diaphana* Gmelin, and *Nuculana bicuspidata* Gould.

The periwinkle, *Littorina cingulifera* Dunker, had apparently succeeded in establishing itself on rocks exposed to violent wave action. Colonies of them were observed in just such situations. The surf-beaten intertidal zone was practically devoid of living mollusks excepting a few bivalves, *Donax rugosus* L.

Mangrove swamp communities

The mangrove swamp communities are characteristic of the estuarine habitats. They are found on muddy flat shores throughout the tropics and are especially abundant near the mouths of rivers and in lagoons where the water table is above or at the surface of the ground. These low-land brackish or salt swamps of the Liberian coast form a distinct community, the mangrove forest. The trees, which stand on high arched prop roots, are from 25 to 40 feet in height. Their main stem is lifted above high tide by the prop roots. At low tide an almost impenetrable tangle of roots may be seen forming the ground story of this forest. These roots hold debris that floats in with the tide until it decays. Aeration is difficult in the waterlogged saline mud, and some of the mangroves (*Avicennia nitida* Jacq.) have developed slender pneumatophores.

Mangrove forests are not extensive in Liberia. They are limited to very narrow belts rarely more than ½ mile wide along the coast line and the lower courses of the rivers whose mucky bottom offers an ideal foot-hold for their highly salt-tolerant rhizophores. The climate in this belt is hot and damp. And, although the rainfall may be as much as 170 inches, it is not an important factor in the development of this forest since it grows upon land which is flooded by sea water at high tide.

Other plants associated with the mangroves are *Conocarpus erectus* Jacq., a shrub 10 feet high, and *Laguncularia racemosa* Gaertn., a glabrous tree 30 feet in height. The transitional zone is composed of salt water ferns, *Acrostichum aureum* L., whose fronds reach as much as 5 feet in length, and false date palms, *Phoenix reclinata*.

The red mangrove, *Rhizophora racemosa* G. F. W. Meyers, makes up about 95 per cent of the total vegetation in the mangrove forest. The black mangrove, *Avicennia nitida,* is present to the extent of a few per cent of the total vegetation and appears to be localized on the edges of the nearly pure stands of *Rhizophora*.

Mangrove forests in tropical Africa have been described by Hutchinson and Dalziel (1927, 1931), Edwards (1940), and Warner (1945).

Savanna

The sandy flats behind the beach and among the mangroves are covered with a low vegetation, mostly grasses 3 to 4 feet high, and scattered trees. This belt, from 5 to 10 miles in width, extends parallel to the coast. It is dominated by such tussock formers as *Andropogon* spp., and the imperator grass, *Imperata cylindrica* (L.) Beauv., which is 4 feet tall. Although grasses dominate the aspect, the small rosaceous tree, *Paranarium macrophyllum* Aubl., and the oil palm, *Elaeis guineensis* Jacq., are conspicuous, the former occurring as widely scattered individuals, the latter in scattered sparse stands. Warner (1945) states that *P. macrophyllum* is the only tree in this savanna which apparently is able to withstand the heat of the grass fire. A savanna with scattered trees and grasses has also been described by Edwards (1940) for Kenya.

The soil of the savanna in Liberia is different from that of the rain forest. It is chiefly sandy and definitely less fertile, has a much smaller water-holding capacity and is therefore drier. Where lateritic soil is encountered the grasses are much higher than those growing in the sand.

The sand plain on which the grasses are established has a true water table which is near the surface only in the rainy season.

The coastal savanna lies in a region of heavy rainfall and is subject to seasonal inundation. Growth is rapid but during the "dry" period the grasses die back. In many places they are burned during the "dry" season and the resulting ashes add fertilizer to the soil which is very deficient in minerals. On account of this continued burning and progressive impoverishment of the soil the savanna is extending at the expense of the forest whose borders are destroyed by fire at the height of every "dry" period and replaced by the grasses. This is a characteristic feature of the landscape.

Inland, on restricted areas near the French Guinea frontier, a type of savanna occurs which has shrubs very widely scattered in the grassland. According to Hutchinson and Dalziel (1926, 1931) this type of vegetation extends through Ubangui-Shari to the Eastern Sudan, Abyssinia, East Africa to Rhodesia and in the Katanga region of the Belgian Congo, and the greater part of Angola. Bequaert (1946) described this type of savanna as covering about 500 square miles in Liberia with tall species of *Panicum* and *Andropogon* as dominants and with occasional stretches of elephant grass (*Pennisetum guineensis*).

Tropical rain forest

The tropical rain forest is the climax vegetation for nearly all of Liberia. It covers about 75 per cent of that country and is part of the great forest that extends from Sierra Leone on the north to the mouth of the Congo. Richards (1939) has written a good description of the floristic composition and structure of this forest. It is the most luxuriant vegetation on the continent of Africa and is the result of large rainfall and high temperatures. In Liberia the rainfall is one of the highest on the whole continent of Africa, averaging 145 inches per year.

The rain forest becomes less dense in the northern portion of Liberia where the annual precipitation is about one third of that which occurs along the coastal region where natives have cleared by burning extensive areas of the land for cultivation. The effect of years of clearing has been to destroy much of the original forest cover. Practically every year edges of this forest have been swept by fire made possible by a drought period of six months. This, together with the felling of trees and the clearing of extensive areas for crops, has brought about a complete change in the ground cover. Along the streams and rivers and in the wetter parts of the tropical rain forest occurs a special plant community, the *Pandanus-Raphia* association.

The tropical rain forest in Liberia is essentially a mesophytic forest of evergreen hardwood trees. Although the majority of them shed their leaves fairly steadily throughout the year there are a few which lose all their leaves at once, *e.g. Casearia dinklagei* Gilg., but produce new foliage simultaneously so that they are never bare. There are some which are bare for more or less longer periods, *e.g. Ceiba pentandra* Gaertn., and *Terminalia superba* Engl. & Diels. As a result of the continual addition and fall of leaves the forest is never bare or without foliage. There is a paucity of humus or leaf mold. This is probably because termites, ants, and fungi destroy it nearly as fast as it forms.

The rain forest is characterized by a close grouping of tall trees (up to 150 feet in height) and a dense understory of smaller trees. The result is a dense canopy of shade with diffused light underneath.

Trees in the Liberian rain forest may be regarded as forming three strata made of first-, second-, and third-story trees. The first-story trees are about 70 to 150 feet high; the second-story from 50 to 75 feet high; and the third-story about 25 feet high.

Typical first-story trees are: *Afzelia bracteata* T. Vogel, 70 to 80 feet tall and with large branches forming heavy crowns; *Lophira alata* Banks, over 100 feet in height with full spreading crowns and low buttresses; *Macrolobium macrophyllum* Macbr., which attains a height of 125 feet; *Ceiba pentandra* Gaertn., 150 feet in height and with large plank-buttresses extending 20 feet upward; and *Erythrophloeum guineensis* G. Don, 125 feet in height and with low buttresses. The crowns of these trees are more or less umbrella-shaped and are supported by an intricate system of branches. Many of the roots of these large trees are on the surface where they spread in all directions rather than grow down. Others, as a result of the hard granite rock, penetrate to a depth of only 6 or 7 feet below the surface. Passage is made very difficult by the exposed roots many of which interlace with one another.

The second-story species, *e.g.*, consist of: *Xylopia aethiopica* A. Rich, 50 feet high; *X. quintasii* Eng. & Diels., about 75 feet in height; *X. staudtii* Engl., 70 feet high; *Strombosia pustulata* Oliv., 60 feet tall; and *Diospyros gabunensis* Gürke, 50 feet high and with low buttresses. The crowns of the second-story trees are usually small and somewhat rounded.

Examples of third-story species are: *Pleiocarpa mutica* Benth., about 25 feet tall; *Voacanga bracteata* Stapf, 20 feet high; and *Rauwolfia vomitoria* Afz., about 18 feet in height. Crowns of these trees are conical in shape. Their slender trunks are never appreciably buttressed.

TABLE II. *Kinds of insects classified according to orders and families and their occurrence in the various vegetation types*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
DIPTERA							
Culicidae	Aëdes africanus (Theob.)			×	×	×	
	Aëdes aegypti (Theob.)			×	×	×	
	Aëdes (Aediomorphus) sp. nr. filis I. & M.			×	×	×	
	Aëdes luteocephalus Newst.			×	×	×	
	Aëdes vittatus (Bigot)			×	×	×	
	Anopheles funestus Giles				×		
	Anopheles gambiae Giles			×	×	×	×
	Anopheles hancocki Edw.				×	×	
	Anopheles nili (Theob.)				×		
	Anopheles paludis Theob.				×		
	Culex annulirostris consimilis Newst.				×	×	
	Culex bitaeniorhynchus Giles				×	×	
	Culex guiarti Blanch.				×	×	
	Culex moucheti Evans				×	×	
	Culex nebulosus Theob.				×	×	
	Culex tigripes Gr. & Ch.				×	×	
	Eretmapodites chrysogaster Graham				×		
	Ficalbia (Miomyia) sp.				×		
	Mansonia africana (Theob.)			×	×	×	
	Mansonia metallica (Theob.)			×	×		
	Mansonia uniformis (Theob.)			×	×	×	
	Megarhinus sp. prob. brevipalpi conradti Grünb.			×	×	×	
Tabanidae	Chrysops longicornis Walk.				×	×	
	Haematopota furians Edw.				×		
	Haematopota guineensis Bigot.				×	×	
	Tabanus besti var. arbucklei Austen				×		
	Tabanus par Walk				×		
	Tabanus postacutus Oldroyd				×	×	
	Tabanus taeniola Palis de B.				×	×	
	Thaumastocera akwa Grünb.				×	×	

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
DIPTERA—*Continued*							
Calliphoridae	Bengalia africana Mall				×		
	Bengalia aliena Mall				×		
	Chrysomya inclinata Wlk.				×		
	Chrysomya putoria (Wd.)				×		
	Rhinia apicalis Wd.				×		
	Strongyloneura dubiosa (Vill.)				×		
	Tricyclea var. bivittata Curr.				×	×	
	Tricyclea distigma Curr.				×	×	
	Tricyclea evanida Vill.				×	×	
	Tricyclea fasciata (Macq.)				×	×	
	Tricyclea punctata Curr.				×	×	
	Tricyclea unipunctata Curr.				×	×	
	Tricyclodes difficilis Curr.				×		
Muscidae	Atherigona sp. prob. cinariña Seguy				×		
	Atherigona septifemur Mall.				×		
	Atherigona sp. nr. tridentata Mall.				×		
	Brevicosta africana Mall.				×		
	Coenosia sp. prob. pilifemur Stein				×		
	Dichaetomyia hargreavsorum nialana Emden				×		
	Dichaetomyia ovata var. rutila Stein				×		
	Dichaetomyia quadrata lineata Stein				×		
	Morellia sp. nr. abyssinica Seguy				×		
	Morellia cyanicolor Stein				×		
	Musca sorbens Wd.			×	×	×	
	Musca ventrosa Wd.			×	×	×	
	Ochromusca setigera Mall.				×		
	Orthellia nudissima (Lw.)				×		
	Phaonia abnormis Stein				×		
	Pygophora acromiata Speiser				×		
	Pygophora parvipunctata Stein				×		
	Stomoxys brunnipes Grünb.			×	×	×	
	Stomoxys omega Newst.			×	×	×	
	Stomoxys sitiens Rond.			×	×	×	
Glossinidae	Glossina fusca Walk.					×	×
	Glossina nigrofusca Walk.						×
	Glossina palpalis Rob.-Desv.		×			×	×

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus Raphia	Coastal savanna	Tropical rain forest	Fringing forest
DIPTERA—*Continued*							
Syrphidae	Baccha brevis Karsch			×		×	
	Eumerus sp. nov. nr. triangularis Hervé-Basin					×	
	Graptomyza sp. nov.					×	
	Melanostoma annulipes Macq. var. mauritianum Bigot.			×		×	
	Microdon brevicornis Loew			×		×	
	Microdon punctulatus Wied.			×		×	
	Paragus borbonicus Macq.			×		×	
	Protylocera aesacus Walk.			×		×	
	Protylocera dibaphus Walk.			×		×	
	Rhingia caerulescens Loew			×		×	
	Tubifera sp.			×		×	
Stratiomyidae	Ashantina antennata Kertész				×	×	
	Chenonomima particeps End.				×	×	
	Gobertinus picticornis Bigot.				×	×	
	Hermetia illucens (L.)				×	×	
	Neopachygaster sp. nr. congoensis Linder				×	×	
	Plecticus elongatus (F.)					×	
	Tinda nigra (Macq.)				×	×	
Psychodidae	Brunettia albonotata (Brun.)				×	×	
	Telmatoscopus albipunctatus (Will.)				×	×	
Fungivoridae	Cerotelion sp.			×		×	
	Delopsis sp.			×		×	
	Lycoria sp.			×		×	
	Neoempheria sp.			×		×	
	Trichosia sp.			×		×	
Tephritidae	Ceratitis (Pardalaspis) giffardi Bezzi			×	×	×	
	Ceratitis (Pardalaspis) puncta (Wied.)			×	×	×	
	Ceratitis (Trirhithrum) fraterna Munro				×	×	
	Ceratitis (Trirhithrum) nigerrima (Bezzi)				×	×	
	Dacus armatus F.				×	×	
	Dacus punctatifrons Karsch				×	×	
Tipulidae	Elephantomyia sp.			×		×	
	Lecteria sp.					×	
	Megistocera sp.					×	
	Tipula sp.					×	
	Trentepohlia exornata Berg.					×	

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
DIPTERA—*Continued*							
Lauxaniidae	Amphicyphus africanus Curr.			×	×	×	
	Homoneura chapini Curr.			×	×	×	
	Homoneura loewi Mall.			×	×	×	
Dorilaidae	Dorilas sp.					×	
Lonchaeidae	Carpolonchaea plumosissima (Bezzi)				×	×	
	Lamprolonchaea aurea (Maca.)				×	×	
	Lonchaea claripennis Maca.				×	×	
	Lonchaea impressifrons Bezzi				×	×	
Tylidae	Mimegralla congoensis Curr.				×		
	Mimegralla conradti (End.)				×		
	Mimegralla trifasciata (Bigot)				×		
Sarcophagidae	Sarcophaga sp.	×			×	×	
Larvaevoridae	Actia sp.				×		
	Aulacephalopsis badia (Gerst.)				×		
	Bequaertiana sp. prob. argyiventris Curr.				×		
	Microphthalma sp.				×		
Rhagionidae	Suragina sp.	×			×	×	
Neriidae	Chaetomerius latifemur End.				×		
Chloropidae	Psilacrum giganteum (End.)				×		
	Rhodisiella tarsalis Ad.				×	×	
Clusiidae	Heteromeringia sp.			×		×	
Conopidae	Stylogaster sp.				×		
Bibionidae	Plecia sp.			×	×		
Asilidae	Ommatius sp. nov.				×		
Heleidae	Forcipomyia sp.			×		×	
Sepsidae	Themira sp.				×		

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
DIPTERA—*Continued*							
Boboridae	Leptocera venalicia (O. S.)					×	
Ephydridae	Paralimna sp.	×	×			×	×
Sciomyzidae	Sepedon sp.					×	×
Tendipedidae	Tendipes sp.					×	
Diopsidae	Diopsis apicalis Dalm.					×	
	Diopsis sp. nr. collaris Westw.					×	
	Diopsis thoracica Westw.					×	
HYMENOPTERA							
Braconidae	Iphiaulux sp.				×	×	
Scoliidae	Campsomeris albicollis (Chr.)			×	×	×	
Chrysididae	Chrysis cincta F.				×	×	
	Chrysis lyncea F.				×	×	
Formicidae	Cremastogaster sp.				×	×	
	Dorylus (Dorylus) gribodoi Emery			×	×	×	
	Dorylus (Anomma) nigricans Illiger			×	×	×	
	Oecophylla longinoda var. fusca Emery				×	×	
	Paltothyreus tarsatus (F.)				×	×	
Termitidae	Macrotermes bellicosus (Smeathman)				×	×	
Sphecidae	Bembix sp.	×		×	×	×	
	Chalybion fuscipennis (Sm.)				×	×	
	Chlorion xanthoceros (Ill.)				×	×	
	Dasyproctus sp.				×	×	
	Hoplisoides sp.				×	×	
	Motes croesus (Sm.)				×	×	
	Sceliphron spirifex (L.)				×	×	
	Sphex sp. nr. indutus (Kohl)				×	×	
	Trypoxylon sp.				×	×	

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
HYMENOPTERA—*Continued*							
Apidae	Anthopora cincta F.				×	×	
	Crocisca sp.				×	×	
	Euaspis abdominalis (F.)				×	×	
	Gronoceras praetexta (Vach.)	×			×	×	
	Halictus sp.				×	×	
	Megachile crocutella Ckll.					×	
	Megachile rufipes (F.)					×	
	Mesotrichia biceps (F.)					×	
	Mesotrichia gabonica Vach.				×	×	
	Mesotrichia imitator nigriceps Friese				×	×	
	Mesotrichia modesta (Smith)				×	×	
	Mesotrichia praeusta (Smith)				×	×	
	Mesotrichia torrida (Westw.)				×	×	
	Pachyanthidium xanthostomum Ckll.					×	
	Pasites nigerrima Fr.					×	
	Trigona erythra Schlett					×	
	Trigona (Dactylurina) staudingeri Brib.					×	
	Trigona erythra togoensis Stad.					×	
	Xylocopa sp.			×	×	×	
Ichneumonidae	Anomalon sp.				×		
	Charops sp.				×		
	Idechthis canescens (Grav.)				×		
	Melanichneumon sp.				×		
	Pristomerus sp.				×		
	Xanthocampoplex sp.				×		
	Xanthopimpla sp.				×		
	Zaleptopygus sp.				×		
Pompilidae	Anoplius sp.				×	×	
	Cyphononyx croceicornis (Er.)				×	×	
	Paracyphononyx zonatus (Ill.)				×	×	
	Pseudagenia personata Grib.				×	×	

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
HYMENOPTERA—*Continued*							
Vespidae	Belongaster junceus (F.)	×					
	Polistes marginalis var. ornatus Lep.				×	×	
	Polybiodes tabida (F.)				×	×	
	Ropalidia cincta (Lep.)				×		
	Rygchium albonigrum (J. Bequaert)				×	×	
	Rygchium marginellum (F.)	×			×	×	
	Rygchium synagroides (Sauss.)					×	
	Rygchium ventrale (Sauss.)					×	
	Synagris calida (L.)					×	
	Synagris cornuta (L.)			×		×	
	Synagris spiniventris Ill.	×		×		×	
Chalcidoidea	Brachymeria sp.				×		
	Cleonymus sp.				×		
	Philomides sp.				×		
	Ptinobius sp.				×		
Tiphiidae	Tiphia pedestris Gerst.				×	×	
Mutillidae	Odontomutilla sp.						
	Timulla cyparissa (Sm.)			×	×	×	
				×	×	×	
COLEOPTERA							
Tenebrionidae	Eupezus sp.						
	Odontopus cupreus F.					×	
	Opatrinus sp.					×	
	Prioscelis sp.					×	
Scarabaeidae	Anomala discordabilis Dohrn.					×	
	Anomala imarginata Ohs.				×		
	Apagonia sp.				×		
	Archon centaurus (F.)				×		
	Diplognatha gagates (Forst.)			×	×	×	
	Eulepida sp.				×	×	
	Heteroligus meles Bilb.				×	×	
	Incala lineola Westw.				×	×	
	Odoretus luteipes Cast. teste Ohaus.				×	×	
	Orcytes monoceros Ol.				×	×	
	Pachnoda marginata Drury				×	×	
	Pachnoda tridentata (F.)				×	×	

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
COLEOPTERA—*Continued*							
Cerambycidae	Acanthorus (Tithoes) palini Hope			×		×	
	Callichroma sp.			×		×	
	Europus sp.			×		×	
	Monochamus ruspator (F.)			×		×	
	Sternotomus regalis (F.)			×		×	
Chrysomelidae	Aspidomorpha sp.			×	×	×	
	Callispa sp. nr. nigripes Baly			×	×	×	
	Cryptocephalus sp. nr. dregei Suffr.			×	×	×	
	Galerucella geniculata Harold			×	×	×	
	Hispa sp.			×	×	×	
	Monolepta sp.			×	×	×	
Coccinelidae	Chilocorus schioedtei Muls.			×	×		
	Epilachna assimilis Muls.			×	×		
	Cheilomenes axillaris Ws.			×	×		
Curculionidae	Lixus sp.					×	
	Mechistocerus sp.					×	
	Protocylas sp.					×	
	Rhynchophorus phoeniciensis F.					×	
	Temnoschoita quadripustulata (F.)					×	
Lagriidae	Lagria sp.				×		
Staphylinidae	Paedurus sp.				×		
Carabidae	Anisodactylus sp.			×	×	×	
	Craspedophorus sp.			×	×	×	
	Ochyropus sp.			×	×	×	
	Orthogonus sp.			×	×	×	
	Pheropsophus sp.			×	×	×	
Anthribidae	Gynandrocerus antennalis Lac.					×	
	Phloetrogus sp.					×	
	Polycorynus sp. prob. compressicornis F.					×	

TABLE II—*Continued*

		Outer strand vegetation	Mangrove	Pandanus-Raphia	Coastal savanna	Tropical rain forest	Fringing forest
COLEOPTERA—*Continued*							
Lycidae	Lycus latissimus (L.)				×		
	Lycus sinuatus Dalm.				×		
	Speckia sp.				×		
Hydrophilidae	Sternolopus sp.					×	
Histeridae	Hister sp.					×	
Meloidae	Epicauta sp.					×	
	Zonabris sp.					×	
	Zonitis sp.					×	
Brentidae	Eupsalis sp.				×	×	
ORTHOPTERA							
Blattidae	Leucophaea grandis (Sauss.)			×	×	×	
	Periplaneta australasiae (F.)			×	×	×	
Gryllidae	Gryllotalpa africana Beauv.				×	×	
DERMAPTERA							
Forficulidae	Diaperasticus erythrocephalus (Oliv.)					×	
Labiduridae	Eurollia sp.				×		

There is a layer of shrubs below the lowest tree stratum, and below this a layer of herbs. Although the majority of the individuals in the shrub layer are young trees belonging to the undergrowth tree and higher strata, there are a few species of true shrubs, *e.g.: Drypetes ivorensis* Hutch. & Dalz.; *Phyllanthus profusus* N. E. Brown; *Angylocalyx oligophyllus* Bak. (f.); *Chasalia elongata* Hutch. & Dalz.; *Rinorea liberica* Engl.; *Tarenna nitidula* Hiern.; and *Urophyllum afzellii* Hiern.

In areas where the rain forest has been thinned out this undergrowth becomes very dense and is practically impenetrable but where the forest is undisturbed it is possible to proceed in all directions, even where there are no trails.

The density of the herb stratum, on the other hand, apparently depends chiefly on the shade cast by the canopy—the maximum abundance being attained in portions of the rain forest which have not been disturbed. Many patches of the forest floor are almost entirely concealed by the growth of these plants, especially by such creeping herbs as *Geophila cordiformis* A. Chev., *G. hirsuta* Benth., and *Aniseia uniflora* Choisy.

Tall woody climbers were usually exposed to the sunlight. They extended from tree to tree and thereby interlocked them into an inseparable mass. These plants climb second- and third-story trees and may reach a height of about 50 feet. They were not found in the crowns of the first-story trees. Large woody climbers present in this forest are: *Lonchocarpus cyanescens* Benth., *Milettia lasiantha* Hutch. & Dalz., *Chlamydocarya capitata* Baill., and *Pycanthus dinklagei* Warb. They are abundant wherever the canopy is disturbed. This is probably because they require strong illumination.

The largest trees are indicators of the primary rain forest (Shantz and Marbut 1923). According to Cooper and Record (1931) there are 250 to 300 species of trees in the Liberian rain forest.

Gallery forest

On both sides of the rivers extending northward from the rain forest are found zones of trees, about 100 yards wide, forming a gallery type of forest (Fig. 1). Although similar in composition to the rain forest these trees are not as tall and are more scattered. They ultimately give way to a savanna. The land is rough and hilly and many outcrops of rock occur. *Adansonia digitata* is a characteristic tree in this savanna.

Cultivated land

The agriculture belts in Liberia are the tropical rain forest and the savanna. The forest land is prepared for farming during the relatively dry months. Large forest trees, undergrowth and bush are cut out. This is allowed to dry and then is burned. The soil is prepared for planting by mixing it with the ashes of the vegetation. This area thus becomes very productive.

Rice is the most important crop grown in the rain forest. Other crops are maize, cassava, cucurbits, peanuts, yams and potatoes. Common fruits found here are pineapples, bananas and papayas.

Most of the original rain forest has been destroyed by natives in preparing the land for agriculture. As the land is usually abandoned after a few years it is rapidly overgrown by secondary growth. As a result, little of the original forest is to be found in the populated areas. From the air the forest appears as a patchwork due to various stages of recovery or succession from being burned and cultivated.

Breadfruit, citrus fruits, and avocadoes have been introduced in the coastal region. Small groves of cocoanut trees are also scattered along the coast line, the cocoanut being used mainly as a food. Cacao seedlings have been planted in the Eastern Province, a region well adapted for the cultivation of this plant.

In the savanna cotton, guinea corn (sorghum), and peanuts are grown extensively.

Living facilities and sanitary conditions are poor. Typical native villages consist of huts with mud-daubed walls and leaf-thatched roofs. These dwellings are earth-floored and very poorly ventilated. Departures from this architectural design are few. Human excreta are indiscriminately disposed of on the trails and in the bush. Water is carelessly handled and, in many instances, polluted with refuse, thus making it a common source of enteric infections.

Insects

All the plant communities support large populations of insects but there is much difference in the kind of species constituting the populations in the various vegetation types. In Table II is given a classified list of insects which were collected during the 2-year period of study. They have been classified according to the 6 main types of vegetation.

It will be seen from the table that most of these insects occurred in two or more communities but some of them, particularly among the *Calliphoridae,* the *Muscidae,* and the *Ichneumonidae,* were restricted according to these collections to one type of community, the coastal savanna. The largest number of species was

in the coastal savanna and the tropical rain forest but more time was spent collecting in these communities than in the other vegetation types.

Mosquitoes

Twenty-six species of mosquitoes were found in the coastal savanna (Table II). This belt (Fig. 1) is traversed by large streams that rise in the hinterland and empty into the ocean. These streams are subject to considerable variation in volume and rate of flow and, during the rainy season, become quite turbulent. Numerous pools are left along their courses when they recede.

Anopheles gambiae was found to be the most abundant mosquito in the coastal savanna during the period extending from 1943 to 1945. Other mosquitoes that were fairly abundant in the same period were *A. funestus, Aëdes aegypti, Culex nebulosus, C. moucheti,* and *Mansonia africana.* The total area in which the mosquitoes were breeding was extensive. This was determined by making frequent checks of standing water throughout the region for larvae. The water in these transitory breeding areas is supplied chiefly during the rainy season but more or less completely disappears during the "dry" season. The 1944 season was quite wet, having a total of 170.40 inches of rain. Accordingly, the number of different kinds of biotopes showing mosquito larvae was greatly increased. These biotopes, together with the species of mosquitoes breeding in each, are listed in Table III.

It can be seen from Table III that the mosquito fauna which utilized the small containers was quite constant and did not include any of the anophelines. Six spe-

TABLE III. *Larval biotopes of Liberian mosquitoes*

Species	Biotopes											
	Tree stumps	Leaf bases	Temporary pools	Swamps	Permanent streams	Shallow wells	Artificial containers	Forest pools	Permanent ponds	Ditches	Rice fields	Fallen leaves
Anopheles barberellus										×		
Anopheles cinctus				×								
Anopheles funestus				×						×	×	
Anopheles gambiae			×			×			×	×	×	
Anopheles hancocki				×		×		×		×		
Anopheles hargreavesi				×				×				
Anopheles nili								×		×		
Anopheles obscurus				×				×				
Anopheles paludis				×								
Aëdes (Aedimorphus) sp. nr. filis			×									
Aëdes aegypti	×	×	×			×	×					
Aëdes africanus	×											
Aëdes luteocephalus	×		×									
Aëdes vittatus				×				×		×		
Culex annulirostris consimilis								×				
Culex bitaeniorhynchus	×									×	×	
Culex guiarti				×				×		×		
Culex moucheti	×				×							
Culex nebulosus	×											
Culex tigripes	×	×		×			×			×		
Eretmapodites chrysogaster	×	×										×
Mansonia africanus	×			×					×			
Mansonia metallica	×			×					×			
Mansonia uniformis	×			×					×			
Megarhinus brevipalpis conradti	×											

cies of mosquito larvae were found breeding in only one kind of biotope, while 12 species were found breeding in 3 to 6 kinds of biotopes. The types of biotopes in which most species of mosquito larvae were found were swamps and tree stumps, each one harboring 12 kinds (see also Kerr 1933; Taylor 1934; Haddow 1948). The list of mosquitoes that selected artificial containers is shorter than that found in tree holes. Three species were collected from the axils of banana leaves and one species, *Eretmapodites chrysogaster,* used fallen leaves for its biotope.

Natural catchments utilized by some of the mosquitoes (Table III) for the deposition of ova consisted of: tree holes, leaf axils, mollusk shells (*Achatina* sp.), and fallen leaves. The large palmate leaves of *Musanga smithii* R. Br. formed cup-like structures, thus holding water. The tree holes were chiefly hollow stumps of cut trunks; a few were rot holes in living or dead trees. Artificial containers were: tin cans, jars, bottles, and tire casings. These varied biotopes illustrate the adaptability of the mosquitoes to a wide variety of water surfaces.

Temporary pools were entirely dependent on rainfall. Some of them dried up for one or two days during brief dry periods in the rainy season but became flooded again by rain over night. These pools, formed on bare soil, were free of aquatic vegetation. They dried up completely at the end of the rainy season in October. A slight film of water, when present, was sufficient for the survival of mosquito larvae.

Swamps occurred in areas subject to periodic inundation. Tall trees and dense tangles of thickets produced deep shade around their margins while others, as a result of clearings, were exposed to direct sunlight. *Pistia stratiotes,* the water lettuce, was observed floating on the surface of a few of these swamps.

Winding, sluggish streams with their protective marginal vegetation displayed high production potentials for certain culicines (Table II) and thereby provided ideal breeding places throughout their courses. During periods of undiminished rainfall many of the smaller streams flooded vast stretches of the surrounding areas and formed temporary swamps.

Permanent mosquito-breeding foci found during the "dry" season consisted chiefly of shallow wells. When not fouled by scraps of food the water was usually clear though, at times, slightly turbid. The turbidity increased, however, during the rainy period. Mosquito abatement was prohibited in those wells which were associated with certain ceremonial rites. Accordingly, biotopes of this kind constituted a great menace during the "dry" season—their density of anopheline larvae being consistently high.

Ground surrounding shallow forest pools was usually covered with stumps and variable amounts of decaying vegetable matter. During the "wet" period these pools were especially important in the seasonal maintenance of certain anopheline populations (Table III). During the "dry" season the water evaporated and the ground became sun-baked.

Ponds were shallow bodies of water with emergent, floating, and submerged aquatic vegetation. During the season of heavy rainfall their turbidity increased; there was also a change in the water level. The high biotic potential of the mosquito fauna was well exemplified by the abundance of larvae of *Mansonia* spp. (Table III).

Low bushes that grew on the margins of ditches cast varying amounts of shade along the sides of the running stream; their fallen leaves provided vegetable litter on the bottom. The water, which was not very swift, was usually clear.

Plots were usually plowed for rice in May. The amount of flooding in them varied according to the rainfall. Usually there were isolated pools at one end of the rice plot while the other end was completely flooded. The water began to dry up in October and November when the rice was ready for harvesting. By December the area was dry.

Predation among mosquito larvae was especially exemplified by *Megarhinus conradti*. Larvae of *Mansonia* spp. were associated with the water lettuce, *Pistia stratiotes*. The biotopes with anopheline larvae were usually free from disintegrating organic matter. *Anopheles gambiae* larvae were the only anophelines that showed a distinct preference for sunlight.

Many adult *A. gambiae* were infected with a mite, *Tyrophagus putrescentiae* (Schr.) var. *occiphilus* (Bks.). Careful examination of the infected mosquitoes failed to reveal any measurable injury which may have been caused by these ectoparasites.

TABLE IV. *Seasonal prevalence of* Anopheles gambiae

1944	Inches of rain	Number collected from huts in Bwa village
Jan.	4.22	63
Feb.	.07	13
Mar.	4.72	57
April	3.67	59
May	5.73	61
June	29.70	3,023
July	53.72	4,182
Aug.	18.58	3,279
Sept.	29.57	1,487
Oct.	10.97	528
Nov.	6.59	55
Dec.	2.86	9
Total	170.40	12,816

Seasonal prevalence of *A. gambiae* was mainly associated with rainfall. This correlation (Table IV) was determined from adult mosquito catches made with an aspirator in Bwa village, a native settlement about 2 miles from Roberts Field.

During the "dry" months there was a paucity of breeding places, hence breeding was scanty and relatively few adult mosquitoes were captured. It should be pointed out that although the rainfall during the "dry" period is much less than in the rainy season, it is of especial importance in producing suitable breeding places for *A. gambiae*. Within the region of seasonal occurrence, owing to the dependence of *A. gambiae* on isolated foci, the occurrence of some rainfall during the critical "dry" season is the chief factor in determining the distribution of this mosquito throughout districts remote from permanent water. When steady rains began in May breeding became more extensive. This continued until September. High densities (June, July, and August) indicated that *A. gambiae* had taken advantage of the opportunity for unrestricted breeding at the height of the rainy season (Table IV). Mattingly (1949) also found that this species occurred in large numbers only during the heavy rains (June and July). In the coastal districts of Sierra Leone *A. gambiae* appears in large numbers during July, August, and September (Thompson 1945).

Anopheles gambiae does not reach high densities in the densely shaded rain forest. The limited anopheline fauna is controlled, at least in part, by the flora which is an expression of the climatic conditions that prevail there. Larvae of *A. gambiae* were found in exposed sunlit pools near native villages where the forest had been cleared, and also on the periphery of the rain forest. Rain-water pools were especially favored by this species. A sudden rise in populations of *A. gambiae* was usually evident following the rainfall which always provided temporary pools for breeding. Native settlements built in the clearings of the rain forest among these breeding foci offered sources of human blood for the house-haunting vector.

Larvae of *Anopheles funestus* were found along edges of streams among grass and other vegetation. They were usually taken in small backwaters where the vegetation had an opportunity of establishing itself and extending its range out into the water. In the forest region it appeared that the chief requirement of an area for the survival of *A. funestus* was a small stream, especially one that was permanent.

Tsetse-flies

The tsetse-fly *Glossina palpalis* (Rob.-Dev.) was captured in the mangrove swamps, portions of the rain forest near

the banks of rivers, and the gallery forest in the savanna where there were medium-sized streams (see Fig. 1). This tsetse has been found to be definitely localized in such areas (Yorke and Blacklock 1915; Frew 1929; Morris 1934; Potts 1937; Bequaert 1946). *G. fusca* did not appear to be so dependent on the presence of water. It is restricted to areas of dense shade (Frew 1929; Bequaert 1946). The bionomics of *G. nigrofusca* in Liberia are similar to those of *G. fusca.*

The ambits (boundary zones) in which tsetses live are largely determined by the density of the vegetation (Nash 1933; Jackson 1941; Moggridge 1950).

Blood-sucking insects

Now that there is in progress the development of animal husbandry and agriculture in Liberia it may be well to refer to the tabanids (horse-flies) which were collected there (Table II). Most of them were captured in the open savannas and were quite abundant. It is not certainly known that these tabanids are vectors of diseases of man or livestock, though the possibility of mechanical transmission should not be overlooked. Annoyance caused by their blood-sucking habits could become quite serious to livestock.

Among the tabanids listed in Table II the following are new records for Liberia: *Chrysops longicornis* Macq., *Tabanus postacutus* Oldroyd, *Thaumastocera akwa* Grünb., and *Haematopota furians* Edw.

Of the 21 species of muscoid flies (*Muscidae*) collected in the coastal savanna (Table II), 4 species are fierce blood-suckers. They are: *Stomoxys calcitrans* (L.), *S. omega* Newst., *S. brunnipes* Grünb., and *S. sitiens* Rond. The species of tsetse-flies in Liberia, also notorious blood-sucking flies, have not become adapted to the dry conditions of the sun-lit coastal savannas.

Food habits of insets

Many species of insects were found feeding on various plants. While some of them seemed to exhibit a preference for certain plants, others were not so definitely restricted in their choice of food. The food habits of these insects are shown in Table V.

The avocado is attacked by 2 species of insects, cocoanut by 4, oil palms by 5 and rice by 2.

Ecology of Insect-borne Diseases

Malaria

During the time this study was made Liberia was highly malarial. The situation had become progressively worse in the coastal savanna because the clearing of the vegetation by fire in preparing the land for agriculture led to an increase in the breeding facilities for *Anopheles gambiae* which prefers sunlit pools. Larvae of this mosquito were found in temporary pools, shallow wells, permanent ponds, ditches and rice fields (Table III). *Anopheles gambiae* is the most dangerous vector of malaria in Liberia; it was also the most domestic anopheline encountered. Its habit of resting indoors and its appetite for human blood were causative factors in outbreaks of epidemic malaria (Soper and Wilson 1943). Haddow (1945), on the other hand, gives evidence which shows that in Uganda *A. gambiae* is largely sylvan and zoophilic. Huts in Liberia served the mosquitoes as good shelters from intense sunlight and high temperatures as well as from the wind and torrential rains. Those huts which had been permanently vacated by their human inhabitants yielded few, if any, of these mosquitoes.

Some of the huts had two or three rooms but the walls did not extend to the ceiling or roof. In spite of the incompleteness of the interior of these dwellings, the number of *A. gambiae* captured from "bedrooms" was always greater than that from rooms not used as sleeping quarters. During the month of June (1944) 2,176 specimens of *A. gambiae* were collected in sleeping rooms. Other rooms in these huts in which collections were made during the same period only yielded 847 mosqui-

TABLE V. *Food habits of some insects collected in Liberia*

Insects	Food plants
DIPTERA	
Muscidae	
Atherigona sp. nr. tridentata Mall.	Fruit of avocado.
Tephritidae	
Ceratitis (Pardalaspis) giffardi Bezzi	Fruit of *Sarcocephalus esculentus.*
Ceratitis (Pardalaspis) punctata (Wied.)	Fruit of *Conopharyngia longiflora.*
Dacus punctatifrons Karsch.	Punctures fruit of cucurbits.
HYMENOPTERA	
Apidae	
Mesotrichia albiceps (F.)	*Citrus aurantifolia.*
Mesotrichia imitator nigriceps Friese	*Citrus aurantifolia.*
Mesotrichia torrida (Westw.)	Leaves of *Cola nitida.*
COLEOPTERA	
Anthribidae	
Gynandroceras antennalis Lac.	Trunk of *Elaeis guineensis.*
Chrysomelidae	
Aspidomorpha sp.	Leaves of *Ipomoea batatas.*
Cryptocephalus sp. prob. dregei Suffr.	Grasses.
Monolepta sp.	Leaves of *Cocos nucifera.*
Scarabaeidae	
Diplognatha gagates (Forst.)	Punctures soft fruits.
Pachnoda marginata Drury	Punctures soft fruits.
Archon centaurus (F.)	Leaves of *C. nucifera* and *E. guineensis.*
Heteroligus meles Bilb.	Leaves of *C. nucifera* and *E. guineensis.*
Trochalus sp.	Fruit of avocado.
Orcytes monoceros Ol.	Leaves of *C. nucifera.*
Coccinellidae	
Epilachna assimilis Muls.	Leaves of maize, rice and cotton.
Curculionidae	
Lixus sp.	Leaves and roots of *Amaranthus caudatus.*
Rhynchophorus phoeniciensis F.	Shoots of *Elaeis guineensis.*
Temnoschoita quadripustulata (F.)	Fruit and trunk of *E. guineensis.*
Cerambycidae	
Monochamus ruspator (F.)	Stem borer of *Manihot utilissima.*
Lycidae	
Lycus sinuatus Dalm.	Leaves of *Cola nitida.*
DERMAPTERA	
Forficulidae	
Diaperasticus erythrocephalus (Oliv.)	Leaves of guinea corn, maize and rice.

toes of this species. No obvious relationship existed, however, between the number of individuals sleeping in the "bedrooms" and the number of *A. gambiae.* Although this mosquito formed a large proportion of the anophelines captured (98 per cent), 2 per cent consisted of *A. funestus* and *A. hancocki.* Hocking and MacInnes (1948) found females of both *A. gambiae* and *A. funestus* in buildings in East Africa.

Laboratory examination of thick blood films taken during native malaria surveys revealed that *Plasmodium falciparum* was the chief malaria parasite with a frequency of 98.8 per cent of all infections. The percentage for *P. vivax* was 1.0 and that of *P. malariae* 0.2. It was also noted that the infection fluctuated with the mosquito densities and, during the season of heavy rains (Table IV), became epidemic. There were sufficient gametocyte carriers among the people, especially the children, to insure the continued production of sporozoite-infected *Anopheles gambiae* and, as a consequence, the incidence of malaria was always high.

Many of the preferential breeding places for *Anopheles gambiae* were due directly or indirectly to the activity of the natives. Although rice cultivation creates a constant and uavoidable hazard, much of the

difficulty is due to carelessness or lack of knowledge regarding malaria control.

The staple foods of Liberians are rice, eddoes, palm oil, cassava, yams, and occasionally fish. The two foods grown throughout the country and eaten daily are rice and cassava. After water has accumulated in the rice plots *A. gambiae* breeding begins on an enormous scale. This continues until rice shoots are several inches above the surface of the water and aquatic plants have grown among them. Shade thus produced checks *A. gambiae* breeding but enhances that of *A. funestus* (the second most important malaria vector in Liberia). The relative larval density of the two species appeared to be dependent upon the stage of development of the rice and the aquatic plants. Thompson (1945) found that *A. gambiae* breeding may occur in rice nurseries and rice fields.

Since the opportunities for widespread anopheline breeding in the rain forest were limited because of the dense shade in the heavily forested belt, the incidence of malaria that did exist was probably due to the migration of native gametocyte carriers. The aboriginals are quite nomadic. There is a tremendous influx of them from the hinterland to the coastal centers. They travel on foot and usually attempt to arrive at wayside villages at sundown where they remain over night and thus expose themselves to the bites of infected *Anopheles gambiae* mosquitoes which also find shelter in these huts. In the highly malarial regions of the coastal savanna these natives secure various kinds of jobs, remain several months and then return to their homes in the hinterland. They thereby maintain a relatively constant supply of gametocytes in their home settlements where the anopheline density is not usually very high.

In portions of the savanna near the French Guinea border (Fig. 1) where the rainfall is below that of the rain forest and where there is a drought period, there was a relative scarcity of *A. funestus*. Malaria in this region of low rainfall was transmitted chiefly by *A. gambiae* which can breed in temporary pools. The dry period in this savanna does reduce somewhat the anopheline population and thereby diminishes transmission of malaria parasites. Many native huts were close to the breeding foci which favored the production of the vectors, the result being that the human inhabitants enjoyed neither protection against mosquito bites nor adequate treatment for malaria.

Bancroftian filariasis

The ideal vector for *Wuchereria bancrofti* (the etiologic agent for Bancroftian filariasis) is also *Anopheles gambiae*. Meager clothing worn by the natives and the lack of screening were factors that had an important bearing on filarial infection in view of the night-biting habits of these mosquitoes. Native villages were constructed in the vicinity of rice fields and small sunny pools where much anopheline breeding occurred. Removal of the soil for the construction of their mud-daubed huts also provided man-made breeding places for the vectors. Improvement in housing conditions, especially screening, and the use of bed nets, together with the reduction of breeding foci, would help check the spread of this disease.

African trypanosomiasis

Tsetse-flies, the vectors of human and animal trypanosomiasis, are confined to Wallace's Ethiopian region, *i.e.*, to Africa south of the Sahara. Though five species of tsetses have been reported from Liberia, *Glossina pallicera* Bigot and *G. medicorum* Austen were not found in this study (Table II).

None of the Liberian tsetse-flies have become adapted to the coastal savanna where there is much exposure to intense sunlight. Accordingly, trypanosomiasis is rare in this area. Mangrove swamps located near native villages, however, could be considered feeding grounds as well as resting haunts for *Glossina palpalis* as there was much traffic through them. Tsetse-flies were frequently observed feed-

ing on the backs of native paddlers as they maneuvered their canoes under the fringes of the mangroves along the Du and Farmington Rivers. *G. palpalis* probably finds the shade and cool situations that prevail in mangrove swamps, from which they fly out on passing traffic, suitable environmental factors (Bequaert 1946). It is in the savanna near the northern boundary (Fig. 1), and especially the Western Province, that *G. palpalis* is a constant danger. Here the fly finds favorable haunts in the gallery forests and good feeding grounds. The area is heavily populated with natives and cattle.

One of the important problems to be solved in connection with the economic development of the potential resources of Liberia, particularly in the northwestern part of the country, is the control of tsetse-flies. Though they are widely distributed in Liberia sleeping sickness in epidemic form has only occurred in the Western Province near the French Guinea boundary and the frontier of Sierra Leone (Fig. 1). Apart from the menace of tsetse-flies to the indigenous population, their effect on the development of large areas of land for agricultural practices is also of great importance, for these insects likewise transmit a form of trypanosomiasis that is fatal to domestic animals.

A vegetation-types map of Liberia would be a very useful tool for making detailed studies of the ecology of tsetse-flies. It would facilitate the study of the bionomics of these insects and also increase our knowledge of the climatic features, surface hydrology, and the soils.

Summary

1. The relationships of insects and insect-borne diseases to the vegetation and to other environmental conditions were studied in the field from 1943 to 1945.

2. Liberia has one of the most humid and rainy climates of Africa. The average precipitation in the Central Province near the coast is about 145.62 inches per year. Monthly mean temperatures vary from about 70° F. in January to 82° F. in April and May.

3. The 6 chief vegetation types are the outer strand vegetation, mangrove, Pandanus-Raphia, coastal savanna, tropical rain forest, and gallery (fringing) forest. The most extensive is the tropical rain forest which covers about 75 per cent of the area of Liberia.

4. A total of 186 determined and 76 undetermined (at present) species of insects were collected. They were classified according to order, family, vegetation type, and, for some species, according to biotope. Most of the insects occurred in 2 or more vegetation types. A detailed classification of mosquito larval biotopes is given.

5. Several species of insects were found feeding on a variety of plants, such as the fruit of the avocado, leaves of the cocoanut, shoots and trunk of the oil palm, and the leaves of maize and rice.

6. The most domestic anopheline encountered was *Anopheles gambiae*. It is intensely anthropophilic and the most dangerous malaria vector in Liberia. It was found breeding in a variety of biotopes, and during the rainy season the larvae were found almost everywhere except in fast-running water and pools covered with vegetation. This mosquito also transmitted filariform larvae of *Wuchereria bancrofti*. The second most important malaria vector is *A. funestus*.

7. Examination of thick blood films showed that *Plasmodium falciparum* was the chief malaria parasite with a frequency of 98.8 per cent of all the malarial infections. The percentage for *P. vivax* was 1.0 and that of *P. malariae* 0.2.

8. Of the 3 species of tsetse-flies collected throughout Liberia, *Glossina palpalis* was the sole disseminator of trypanosomiasis. This disease has only occurred in epidemic form in the Western Province of Liberia near the French Guinea boundary and the Sierra Leone frontier.

9. Movements and habits of the people are related to the insect-borne diseases.

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ECOLOGICAL STUDIES OF DATE VARIETIES IN FRENCH NORTH AFRICA[1]

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In an ecological study of date varieties (*Phoenix dactylifera* L.) in French North Africa, the varieties grown in the Sahara under climatic conditions nearly ideal for date culture were compared with those in nearby districts where climatic conditions are marginal but where dates are still the most important crop grown. Water and soil are not discussed here in detail because they are not primary factors limiting the spread of date culture; hence they are of secondary importance in adaptation. The results of this study throw some light on how varieties and culture may be adapted to relatively unfavorable climatic conditions.

According to de Candolle (1886) the date palm has existed from prehistoric times in the warm dry zone which extends from northwest India across Arabia and north Africa, principally between parallels 15° and 30°N. It seems probable, however, that the species originated in the eastern part of this zone and was spread by prehistoric man who, long before its cultivation was begun, utilized the fruit and undoubtedly greatly extended the area over which it originally occurred. Dates are easily transported and seeds grow readily in moist soil in a favorable climate. The nearest relative of the date palm is the so-called wild date, *Phoenix sylvestris* Roxb., of India, a species not easily distinguished botanically from *P. dactylifera*. The earliest known records of date culture are from Sumer, about 3000 B.C., in what is now southern Iraq, and throughout recorded history this area, including adjacent portions of Iran and Arabia, has remained the most important center of date culture in the world. Dates were also cultivated in ancient Egypt and at a very early period in desert oases from southern Iran to northeast Africa. By means of seed carried in fruit, date palms were probably disseminated around the Mediterranean coast by early Phoenician traders, but the introduction of date culture into the Saharan oases of what is now French North Africa is known to have begun near the end of the Roman Empire following certain Berber immigrations and the introduction of the camel in the 6th century A.D. (Gautier 1935).

Geography

French North Africa ranks next to Iraq and the territory around the Persian Gulf in importance as a date-growing area. It is of interest to the student of horticultural ecology because of the wide range of conditions under which dates are grown. The date areas are all located south of the Atlas Mountains, the main system of which extends from a point near the Atlantic Coast in Morocco opposite the Canary Islands for about 1500 miles in a northeasterly direction to that point of the continental bulge in Tunisia which juts out toward Sicily.

Geographically there are four regions where dates are grown: (1) the low

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desert, (2) the high desert, (3) the foothills, and (4) the coast. Most of the dates are produced in regions 1 and 2 where climatic conditions are favorable. Regions 3 and 4 are marginal. There are, of course, some border line districts. Some of the oases in the high desert are marginal for date culture because of low temperatures. The transition from desert oases near the southern slopes of the Atlas system to marginal ones within the foothills is not always abrupt. Also, the most southerly of the large date-growing oases of Algeria—those in the vicinity of In Salah and Timimoun—should, perhaps, be grouped separately, as the elevation there is about 1,000 ft. (intermediate between the low desert and the plateau) and the temperatures are somewhat higher than those in the other date growing oases of French North Africa. Perhaps in that part of the Sahara there are localities marginal for date culture because of excessive heat, but time did not permit studies in that region.

(1) The low desert is a vast depression which extends from the foothills of the Atlas Mountains in the north to the beginning of the central Saharan plateau in the south and from the rising plains which border the Oued Rhir on the west to the coastal hills of Tunisia in the east. At the bottom of this depression and extending east and west across the northern part of it is a series of large shotts, or shallow salt lakes, formed by the drainage of this interior basin, which has no outlet to the sea. The lowest parts of the depression are below sea level. The principal date-growing oases of the low desert are located relatively near to these shotts, or to smaller outlying ones which in event of excessive precipitation may, in some cases, overflow to the larger and lower ones. About half of Algeria's 6.9 million date palms and about two-thirds of Tunisia's 2.5 million are found in the low desert, which make a total for this region in excess of five million palms. There are six large groups of oases: the Oued Rhir, the Zibans, Ourgla, and the Oued Souf in Algeria and the Jerid and the Nefzaoua in Tunisia. Nearly all of the present export of dates from French North Africa is from this region and it is here that date culture is most highly developed (Fig. 1).

(2) West from the Oued Rhir, the elevation increases and forms a plateau

FIG. 1. A Deglet Noor date garden in the low desert area (Oued Rhir) of French North Africa. The ditch is for drainage, necessary because of a high water table.

FIG. 2. Date palms in the foothills of the Atlas Mountains at El Kantara, Algeria, a marginal district.

which extends across Algeria and southern Morocco to the southwest extension of the Atlas system. Exclusive of the oases in the far south as mentioned previously, the principal districts where dates are grown in this region are from east to west: Ghardaia and Colomb-Béchar in Algeria, Figuig just across the border and the valleys of the Ziz (including the so-called Tafilelt) and the Draa in southern Morocco. Most of Morocco's 2.9 million date palms are about equally divided between the two river valleys mentioned.

(3) Into the foothills north of the desert, date culture has been carried as far as it has proved practicable. One of the oldest and one of the largest of the oases in a marginal district of this type in Algeria, is El Kantara, about 35 miles north of Biskra (Fig. 2). Because of its strategic location as the only pass through the mountains in this part of Algeria, El Kantara was at one time an important outpost of the Roman Empire and it was probably one of the first localities of its kind to be planted to dates. The number of palms there is estimated at 84,000.

(4) Although occasional date palms are found here and there along much of the coast of French North Africa, the only place where date culture is given much serious attention is at Gabes, Tunisia. Here the interior desert region of southern Tunisia almost reaches the coast, but is separated from it by a relatively low and narrow range of hills. There are said to be 222,000 date palms at Gabes.

There is a considerable number of date palms on the Island of Djerba about 60 miles east of Gabes, but the greater part of them are grown without irrigation and receive little cultural attention. Thousands of them are found stunted in groups on slopes near the beach, and all across the island there are sparsely scattered palms among olives and in areas devoted largely to grain.

In spite of the fact that climatic conditions at Gabes are marginal for date culture, dates were probably grown there earlier than in any other part of French North Africa. Pliny commented about the luxuriance and productivity of date palms and other crops in this locality, then known as Tecape, whereas the introduction of date culture into the oases of the French Sahara did not begin until near the end of the Roman Empire as stated above.

Climate

The climatic conditions necessary for date culture are well known. The palm makes no vegetative growth until maximum temperatures exceed 50° F (Mason 1925a; Vinson 1914). Pronounced injury to the leaves occurs when temperatures reach 20° F (Nixon 1938), but mature palms have been known to survive a minimum temperature of 4° F (Mason 1925b), although, of course, all leaves were killed. However, temperatures of 20° F and below reduce the leaf area and the fruiting capacity of the palm, and their frequent occurrence imposes a thermal limit to the extension of date culture. The requirements for satisfactory fruit production are high maximum temperatures when the fruit is developing and a rainless period immediately before and during the ripening of the fruit. Because of these requirements, the production of date fruit is limited almost entirely to subtropical desert areas, even though the date palm itself will grow in any tropical or subtropical climate.

In Table I, stations in localities typical of the four regions of date culture in French North Africa are compared with regard to temperature and rainfall. Similar data for Indio, California, the center of date culture in the United States, are added for further comparison. The ripening of dates in any locality is largely dependent upon the sum total of heat during the period when the fruit normally makes most of its growth and reaches the initial ripening stage. For this reason, the average maximum temperatures are given for May to October inclusive, since these data afford a better index to the possibilities for date culture than the average yearly maxima. Likewise, the mean minimum temperatures for the coldest month, January, are given since they are an index to the possible restrictions from low temperatures.

Rainfall is a serious obstacle to date culture if it occurs in the period immediately before and during the early ripening of the fruit. In these stages the fruit is very susceptible to damage from contact with water and long-continued

Table I. *Climatic data for critical periods at stations in French North Africa typical of districts where dates are grown**

Region and station	Average daily air temperature (°F)			Average rainfall (inches)						
	No. yrs. record	Maximum May to Oct. incl.	Minimum Jan.	No. yrs. record	July	Aug.	Sept.	Oct.	4 Mos.	Year
Low Desert										
Touggourt, Algeria	15	96.6	38.1	16	.03	.00	.13	.15	.31	2.26
Tozeur, Tunisia	40	96.1	41.5	10	.00	.08	.20	.16	.44	4.66
High Desert										
Colomb Bechar, Algeria	8	94.0	34.2	6	.01	.09	.14	.64	.88	2.17
Erfoud, Morocco	12	97.5	34.3	12	.00	.08	.28	.47	.83	2.72
Foothill										
El Kantara, Algeria	9	88.5	36.5	16	.09	.24	.65	1.30	2.28	9.71
Coast										
Gabes, Tunisia	40	84.7	42.8	10	.00	.08	.67	1.54	2.29	7.82
U.S.A.										
Indio, Calif.	25	99.7	38.6	53	.05	.22	.21	.18	.66	3.00

* Data for Algeria from Lassere (1932); for Tunisia, temperatures from the local office of the Tunisian Department of Agriculture at Gabes, rainfall from the U. S. Weather Bureau; for Morocco, from the Service de Physique du Globe et de Meteorologie, Casablanca, by correspondence; for Indio, Calif. from U. S. Weather Bureau (1932–37).

high humidity which may cause serious losses from checking, splitting, rotting, and souring. Rainfall is given for the months July to October, inclusive, which covers the critical period for most varieties, and these data are compared with the yearly total.

Touggourt at an elevation of 243 feet may be taken as typical of the low desert and of a nearly ideal date climate. Late-ripening varieties of dates reach perfect maturity; injury to palms from low temperatures is almost unknown; and damage from rain is extremely rare. Climatic conditions are much the same in all the low desert area surrounding the salt lakes or shotts of eastern Algeria and southern Tunisia. Tozeur, elevation 153 feet, is somewhat nearer to outlying foothills of the Atlas system and the rainfall during the critical ripening period is slightly higher, and for the entire year appreciably higher than at Touggourt. Colomb-Béchar at an elevation of 2523 feet in western Algeria and Erfoud at an elevation of 2625 feet on the Ziz River in the Tafilelt district of Morocco may be taken as typical of the high desert. The maximum temperatures for these two stations are fairly high, but there is a definite reduction in minimum temperatures as compared with the low desert. Although the total rainfall from July to October is not high, from the data in Table I there appears to be about twice as much in the high desert as in the low desert.

The foothill region is represented by El Kantara at an elevation of 1880 feet. Maximum temperatures are definitely lower here than in either of the two desert regions. Late-ripening varieties of dates seldom mature. Minimum temperatures are not low enough to restrict date culture, but the high rainfall, in addition to low maximum temperatures, makes this very definitely a marginal locality.

The coast of Tunisia is represented by Gabes which is only a few feet above sea-level. Maximum temperatures for the May to September period are lower at Gabes than at any of the other stations reported. Although the annual rainfall is lower at Gabes than at El Kantara, the rainfall of the two stations for the critical ripening period is remarkably similar. At Gabes late-ripening varieties do not reach maturity; rain damage to the fruit is common; and evidence of continuous high humidity is also afforded by the presence on date leaves of graphiola leaf spot, a fungus disease caused by *Graphiola phoenicis* (Moug.) Poit seldom found in the interior areas.

Varietal Studies

A large number of date varieties are found in French North Africa. The writer studied more than 200 and there are probably that many more. The greater part of these are represented by only a few specimens in a given locality and there is often a question as to their varietal status. Only a few are widely distributed and still fewer are grown in large numbers.

In the present paper, the five most important varieties of the desert regions are compared with the five most important varieties of the marginal districts. There might be some difference of opinion as to the importance of one or two varieties included in the first group, but in the localities studied there were only five outstanding varieties that could possibly be included in the second group.

General information about each variety is given first, followed by a tabulated comparison of the more important fruit and leaf characters.

Varieties grown in the desert regions

1. *Deglet Noor* has long been the chief variety grown for export in the low desert region of French North Africa. Because of its excellence and reputation, it has been tried in many different places, but it has a rather narrow range of adaptation. In Algeria and Tunisia, it is said to be less tolerant of salty soil than other varieties.

2. *Rhars* is the most abundant variety in the low desert region of Algeria; it has a reputation for being resistant to salt and

is often found under very saline conditions.

3. *Deglet Beida* occurs throughout the same range as the Rhars and is the most important dry, or bread, date in that part of Algeria; it does fairly well in saline soils.

4. *Fteemy,* also known as Alligue (Jeangérard 1909), is a staple variety among the natives of southern Tunisia. According to Kearney (1906), it comprises about one-third of all the date palms in the low desert region of Tunisia. In Algeria, occasional specimens are found in the Oued Rhir under the name of Bou Arrous. Fteemy was also found by the writer to be very similar to, if not identical with, the Hamraya of Biskra, which was introduced into the United States and has been described in another publication (Nixon 1950). Notes on the variety in the United States agree with those made subsequently in Algeria and Tunisia except that the ripening here has apparently been somewhat earlier than that reported in Tunisia, but the small number of palms in this country have not afforded adequate observations.

5. *Bou Feggous,* sometimes listed simply as Feggous, is the most widely grown variety in southern Morocco, and is well known in western Algeria. It is not the variety grown under this name in Tunisia.

Varieties grown in marginal localities

According to the local office of the Tunisian Department of Agriculture, in the vicinity of Gabes there are approximately 222,000 palms, of which 122,000 are seedlings and 100,000 are named varieties. Of the named varieties 36,900 are Kenta, 34,500 Aguewa, and 26,500 Bouhatem.

1. *Kenta* is rated as the best and most productive of the three principal varieties at Gabes, but as the least tolerant of salty soil. In the desert it is given a higher rating for salt-resistance (Kearney 1906). The Kenta variety is widely grown in Tunisia; it is not common in Algeria, but a few specimens under this name were introduced from there into the United States (Nixon 1950). The palms as grown in Coachella Valley, Calif., are very similar to those seen at Gabes, except that they are somewhat less vigorous, the pinnae are longer, and the fruit is somewhat smaller and slightly later in ripening.

2. *Aguewa* ranks second in importance at Gabes and of the three principal varieties it is said to be the most tolerant of salty soil. The palm is similar to Kenta, but the leaves are a little shorter, the pinnae are somewhat narrower, and the color of the foliage is slightly more yellowish.

3. *Bouhatem* also is similar to Kenta, but it ripens slightly earlier; the fruit is a trifle softer, although still classed as a dry date, and it is said to show somewhat less spoilage following rain. The foliage is a little darker green than that of the other two principal varieties at Gabes.

4. *Lemsi* is the only variety found in large numbers on the island of Djerba. It is rated as the most salt-resistant variety on the coast of Tunisia. Much of the fruit is consumed in the *khalal,* or prepipe, stage.

5. *Bouzeroua* is a variety grown only in the foothill oasis of El Kantara, Algeria, where it is said to constitute about two-thirds of the estimated 84,000 palms in this locality.

Explanation of variety descriptions

Descriptive data from studies of the above varieties in French North Africa are given in Tables II and III. Information as to time of ripening and rain tolerance of the different varieties was obtained from local authorities in the districts where they are grown and in the case of the Deglet Noor, Rhars, and Deglet Beida, it could be supplemented by observations previously made in the United States. Descriptive terms are, of course, relative. All varieties of dates, for example, will be damaged by rains occurring during the critical period of ripening and no fruit would survive rainfall more or less continuous dur-

TABLE II. *Five most important date varieties in the Sahara Desert of French North Africa*

Variety	Deglet Noor	Rhars	Deglet Beida	Fteemy	Bou Feggous
Fruit					
Type	semidry	soft	dry	soft	soft
Time of ripening	late	early	midseason	late	midseason
Rain tolerance	poor	poor	good	poor	fair
Size	medium	medium	medium	medium	medium
Shape	oblong-ovate	narrowly oblong-obovate	oblong	oblong-ovate	oblong-oval
Color: *khalal*	light red	yellow	yellow	red	yellow
tamar	amber brown	reddish brown	light buff	dark reddish brown	reddish brown
Leaves					
Curvature*	SE	PO	PO	MO	SE
Blade length	400–473	323–432	406–418	342–463	300–414
Spine area (per cent)	24–35	15–25	18–22	25–34	16–25
Spines: number	40–55	23–43	29–47	46–52	27–41
length, maximum (cm)	12–19	14–19	12–15	14–16	14–22
rachis angles, max. (degrees)	15–40	15–40	30–90	35–60	30–50
Pinnae: droop	slight	slight	medium	medium	medium
longest (cm)	57–83	53–58	59–66	54–65	59–75
widest (cm)	3.1–3.7	4.5–5.1	3.8–4.1	3.8–4.2	3.9–4.9
terminal (cm)	31–50	14–23	22–23	24–30	19–22
rachis angles in lower blade, maximum (degrees)	20–50	30–45	30–50	30–45	30–60
basal spacing index (per cent)	40–75	55–95	50–65	50–65	50–75

* S—slight; M—moderate; P—pronounced; E—evenly distributed; O—increasing outward.

ing this period, but varieties do vary in the amount of damage caused by occasional rains.

Fruit of all the varieties was seen and studied by the writer, but Tunisia and Morocco were visited too late to see fruit in the *khalal,* or preripe stage, when the fruit is a shade of red or yellow characteristic of the variety in question. After dates have ripened and dried sufficiently to be handled without danger of fermentation and souring, they are in the *tamar* stage, familiar to American and European consumers of imported dates. No descriptive data for the fruitstalks are included because all the bunches had been removed from the palms of the marginal varieties prior to the writer's visit to these districts.

Numerous observations of the leaf characters of the different varieties were made on palms of different ages under a wide range of conditions, but the actual measurements given represent leaves taken from two or more palms, 10 to 20 feet high, occasionally somewhat higher, in fair to good condition, and representative of the

TABLE III. *Five most important date varieties in marginal districts of French North Africa*

Variety	Kenta	Bouhatem	Aguewa	Bouzeroua	Lemsi
Fruit					
Type	dry	dry	semidry	dry	dry
Time of ripening	early	early	early	early	early
Rain tolerance	good	good	fair	good	good
Size	medium	small	small	medium	medium
Shape	oblong-oval	oblong-oval	oblong-oval	oblong-ovate	oblong-ovate
Color: *khalal*	yellow	yellow	yellow	yellow	red
tamar	dull brown	reddish brown	reddish brown	yellowish brown	reddish brown
Leaves					
Curvature*	MO	MO	MO	PO	SO
Blade length	465–497	329–433	333–404	312–389	337–446
Spine area (per cent)	5–12	6–10	12–19	15–17	23–27
Spines: number	18–22	22–25	18–22	20–28	29–45
length, maximum (cm)	12–14	7–12	9–10	8–12	12–14
rachis angles, max. (degrees)	50–65	80–100	30–45	40–80	25–45
Pinnae: droop	medium	medium	medium	slight	slight
longest (cm)	53–57	46–52	48–62	59–62	46–58
widest (cm)	3.6–4.6	2.8–3.9	3.0–3.8	3.1–3.3	3.9–4.4
terminal (cm)	35–37	28–32	33–47	30–43	23–32
rachis angles in lower blade, maximum (degrees)	50–80	70–90	35–55	45–75	30–40
basal spacing index (per cent)	20–30	15–30	30–45	30–45	35–45

* S—slight; M—moderate; P—pronounced; E—evenly distributed; O—increasing outward.

period after maximum size of leaves and productivity of palms have been reached. The spine area is measured on the rachis from the first proximal spine to the last distal spine and expressed as a percentage of the blade length as measured from the first proximal spine to the tip of the terminal pinna. The angles formed by the spines with the distal extension of the rachis are designated "rachis angles." The rachis angles of the pinnae are measured similarly, but only for the first 10 or 12 proximal groups. The basal spacing index is the proportion of lineal space on the rachis occupied by the first 6 to 8 proximal groups of pinnae. A basal spacing index of 50 per cent indicates that the lineal distance between the groups is equal to that occupied by the groups; the higher the index the less space between the groups and the lower the index the more widely they are separated. These leaf characters have been described and evaluated in detail in another publication (Nixon 1950).

Discussion

Fruit

The five varieties grown in the marginal localities have without exception fruit of the dry, or relatively dry type, which is comparatively early in ripening. Early ripening is another way of saying that a shorter season, or less heat, is required to bring the fruit to maturity. It has already been shown in Table I that maximum temperatures are lower in these marginal localities than in the desert areas and in both of them it has been found that late-ripening varieties like the much-prized Deglet Noor will not mature satisfactorily. Early ripening aids adaptation in another way. The rainfall data show that the likelihood of rain increases in the fall. All date varieties are damaged more or less by rain, but early ripening ones will be harvested before they are exposed to very much rain. The consumption of much of the fruit of the Lemsi variety in the *khalal* stage, immediately preceding final ripening, would also favor adaptation by earlier removal of the crop and avoidance of late fall rains. The dry texture of the fruit is another character favoring adaptation; because of the low moisture content such fruit is less subject to fermentation and souring and to fruit rots than the soft varieties.

On the other hand, of the five varieties from the desert areas only one, Rhars, is early-ripening, and two, Deglet Noor and Fteemy, are definitely late. Only one of the varieties, Deglet Beida, is dry, and it is the least extensively planted of the five. Rhars, Fteemy, and Bou Feggous are soft, and Deglet Noor is semidry in texture. Rhars, Fteemy, and Deglet Noor are all very susceptible to damage from rain or high humidity.

There do not appear to be any consistent differences in size, shape, and color of fruit between the desert varieties and the marginal varieties.

Leaves

The possible relation of leaf characters to adaptation is uncertain, but attention may be called to some differences which seem to be more or less characteristic among the varieties studied. From the data in Tables II and III, it is apparent that the marginal varieties except Lemsi have short spine areas (5–19 per cent of blade length); the spines are short and few to medium in number (18–28); they are slender and flexible. The desert varieties on the other hand, have medium to long spine areas (15–35 percent of blade length); the spines average longer than those of the marginal varieties; they are medium to heavy in weight. Figure 3 illustrates these differences. Among the desert varieties, the spines of Deglet Noor and Fteemy are numerous (40–55) and those of Deglet Beida, Rhars and Bou Feggous moderate to numerous (23–47).

The basal groups of pinnae of all the marginal varieties are widely separated (basal spacing index of 15–45 per cent) as compared with the desert varieties (basal spacing index of 40–95 per cent). In the marginal varieties, the length of the

FIG. 3. Lower portions of date leaves showing (A) the long spine area and numerous heavy spines of the Deglet Noor variety as contrasted with (B) the short spine area and few slender spines of the Kenta variety.

terminal pinna is greater than ½ that of the longest pinnae, whereas in the desert varieties, except Deglet Noor, the terminal pinna is less than ½ the length of the longest.

The leaves of the Lemsi variety resemble those of the desert varieties as regards length of spine area, number and character of spines, and rachis angles of both spines and pinnae. The Lemsi variety has been planted in quantity only under special conditions where salt tolerance is said to be the chief and limiting varietal qualification on the island of Djerba off the coast of Tunisia. Whether salt tolerance has any relation to these characters of the leaves is not known, but rather high salinity is characteristic of most of the soil and water where the desert varieties are grown.

There do not appear to be any consistent differences in the curvature of the leaves and the droop of the pinnae between the desert varieties and the marginal varieties. Although measurements of the widest pinnae do not show consistent differences, observations, supported by later examination of photographs, seemed to indicate that the proximal pinnae of the marginal varieties, except Lemsi, were narrower than those of the desert varieties.

In connection with leaf characters, two incidental observations were recorded. Less red date scale (*Phoenicococcus marlatti* Ckll.) was found on leaves with widely separated groups of basal pinnae than on those with more crowded groups. This scale occurs under overlapping leaf bases, but its chief place of lodgment on the leaf blade is in the pockets formed by the folds of the pinnae at the point of attachment to the rachis; these pockets are longer and afford more protection to the scale on leaves with small rachis angles than on those with large rachis angles. The wide separation of pinnae groups also appears to favor more ventilation and exposure in the crown of the palm and it is possible that this might serve to reduce the incidence of graphiola leaf spot. This fungus is found on date leaves where the atmospheric humidity is continuously relatively high, as at Gabes, and may reduce the bearing capacity of palms by causing the early death of leaves. Not enough of either the scale or the fungus was seen to indicate that they were causing serious injury to the foliage at the time of the writer's visit. Yet it is conceivable that factors such as these may have contributed to varietal adaptation during a cycle of more humid years or in other more humid localities where the varietal types grown at Gabes might have originated.

It was apparent from these studies that any differences in the characters of the most important date varieties grown in the Sahara Desert as compared with those in marginal districts of French North Africa are the result of selection by man over a long period of time, although it is not likely that there was any conscious selection of leaf characters as there probably was of fruit characters. Among the many different minor varieties and seedling palms in the marginal districts, the range of variation appears to be comparable to that found in the desert regions.

Similarity of marginal varieties

The three varieties that account for about 98 per cent of the variety plantings

FIG. 4. Date palms at Elche, Spain, showing method of planting similar to that at Gabes, Tunisia. In these marginal districts palms are arranged in border rows around plots in which low-growing crops are planted.

at Gabes are very similar in both leaf and fruit characters. The writer was there ten days before he could distinguish the palms and even then it required close observation. The differences are not pronounced or obvious upon casual inspection. A common origin seems likely. As Kenta is said to be distributed throughout southern Tunisia, whereas Aguewa and Bouhatem are found only in the vicinity of Gabes, it is possible that Kenta is the parent variety and that the other two originated as seedlings from it.

The Bouzeroua of El Kantara is also very similar in its leaf and fruit characters to the three varieties of Gabes. It is possible that this may be more than a coincidence. Both Gabes and El Kantara were occupied by the Romans for several centuries and there was communication between the two places over a foothill route via Biskra, Algeria. As mentioned previously, date palms are known to have been grown at Gabes during this period, so that dates from Gabes may have been the source of seeds which produced the date palms at El Kantara.

Method of planting at Gabes

Another factor of importance in adapting date culture to humid conditions at Gabes is the method of planting. Instead of conventional orchard arrangements, palms are regularly planted 10 to 15 feet apart in one or two rows around rectangular garden plots. The size of the gardens varies from as small as about one-eight of an acre to one or two acres, most of them being about half an acre in size. In the centers of the gardens, vegetables or low-growing crops are grown. This method of planting always permits light and aeration on one or both sides of the palm, and serves to minimize losses from fruit rot and to reduce the incidence of graphiola fungus on the leaves. Palms could undoubtedly be planted in this way to advantage in some localities in the United States, such as the Salt River Valley, Arizona, and in southwest Texas. It has repeatedly been observed that in periods of humid weather, damage from fruit rot is much less on outside palms than on inside palms. What is more logical than to eliminate the inside palms!

This same method of planting is also used in the date gardens at Elche, Spain (Fig. 4), where climatic conditions are even more marginal for date culture than at Gabes. Since the plantings at Elche are believed to have originated in Phoenician times, the similarity in arrangement of palms at Elche and Gabes may have been due to a common origin.

Summary

A study of the five most important date varieties of the desert areas of French North Africa compared to the five most important varieties of marginal districts in Algeria and Tunisia indicates that adaptation to lower maximum temperatures during the growing season and to increasing precipitation in the fall is favored by early ripening and dry character of fruit. Four of the five marginal varieties have fewer spines and all of them have more widely separated basal groups of pinnae than the desert varieties; these characters may play some part in adaptation and, along with other similarities, suggest the possibility of a common origin of these varieties. Planting in border rows around garden plots in the centers of which low-growing fruits and vegetables are grown, as at Gabes, provides a maximum exposure of palms and fruit to sunlight and aeration and is probably an important factor in adapting date culture to relatively humid conditions.

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ECOLOGICAL STUDIES OF BREEDING BIRD POPULATIONS IN NORTHERN MAINE

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Field studies of the ecology of the breeding birds in northern Maine were conducted by the authors during the early summer of 1949. These studies were made during the period June 3 to July 11 inclusive, in the vicinity of the village of Guerette, located about 16 miles southeast of Fort Kent, Aroostook County, in the extreme northern tip of Maine. The region investigated covered most of the area within a radius of 8 miles of Guerette and included Square, Cross, Mud and Long Lakes, and the northern edge of Madawaska Lake. Much of the information obtained was accumulated in conjunction with detailed studies to determine the degree of control exerted by natural breeding bird populations of the boreal spruce-fir forest on a moderate infestation of the spruce budworm (*Choristoneura fumiferana* Clem.). The results of this work will appear in a separate report.

BIOTIC COMMUNITIES

General surveys were made of the entire region in order to obtain information on the habitat distribution of the breeding birds. All or practically all of the habitat types occurring in the region were inspected. Detailed list counts were made in most of these for the purpose of determining the species composition and relative abundance of birds in each community.

Many of the characteristic birds of the biotic communities in both the hemlock-hardwood region and the boreal spruce-fir forest region (as defined by Oosting 1948) were found to be present in northern Maine. These two regions correspond to the Transition and Canadian life zones of Merriam (1898); to the Canadian and Hudsonian biotic provinces of Dice (1943); and to the deciduous forest-coniferous forest ecotone and coniferous forest biome (Clements and Shelford 1939). The majority of the species in the communities on top of the hills and ridges were those typical of the hemlock-hardwood region while the communities on the extensive lowland areas were composed predominantly of species characteristic of the boreal forest region. On the intermediate slopes most of the communities were essentially mixed in character. Since these slopes were more mesophytic that either the hilltops or the lowland areas, the mature ecotonal forest that develops on them, *i.e.*, the mixed hemlock-hardwood-boreal forest, probably represents the climax community for the area. This being the case, the mature spruce-fir boreal forest of the lowland might be considered a post-climax, and the mature hemlock-hardwood forest of the hilltops and ridges could be considered a pre-climax community (Weaver and Clements 1938).

In the descriptions of the avian communities that follow, the characteristic birds of each usually have been listed as *primary, secondary,* or *minor* species. These divisions roughly indicate the relative importance of the various species in the community, based on their abundance and size. The birds listed under each of these headings are arranged in the order of their taxonomic classification. In the description of the habitats the scientific and common names of plants are taken from Gray's Manual of Botany (Fernald 1950). Numerical status of plant species was determined by transect counts in the forest areas and by general survey in the scrub areas. In all hydrarch communities the modifying term "bog" is used to signify its relationship to a boreal hydrosere, rather than swamp, which term may be restricted to hydroseres of more southern type (see Aldrich 1943: 347).

Boreal spruce-fir forest community

The birds of the boreal spruce-fir forests were studied much more intensively than those of other communities. Extensive areas of second-growth spruce-fir forest in various stages of development, following lumbering, were present on the lowlands. Coniferous trees ordinarily constituted between 80 per cent and 95 per cent of the overstory in this type. The primary tree species were balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*). These two species were quite variable in their relative abundance. On poorly drained sites black spruce was often present in nearly pure stands, while on better drained areas, balsam fir usually predominated. Secondary tree species in this forest included red spruce (*Picea rubens*), white spruce (*Picea glauca*), white cedar (*Thuja occidentalis*), quaking aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and red maple (*Acer rubrum*). Species of minor importance that occurred only as occasional, scattered individuals included tamarack (*Larix laricina*), white pine (*Pinus strobus*), and yellow birch (*Betula lutea*). The vegetation of the understory and forest floor was largely dependent on the density of the canopy. In spruce-fir stands with a closed canopy, the forest floor was usually covered with a dense mat of mosses and leafy liverworts, while the brush understory and herbaceous layer were only sparsely represented. In the more open stands, however, both the understory brush and herbaceous vegetation were much more prominent. Mountain maple (*Acer spicatum*) was often common in the understory mixed with saplings of conifers, while some of the common herbaceous plants were: corn-lily (*Clintonia borealis*), dwarf cornel (*Cornus canadensis*), wild lily-of-the-valley (*Maianthemum canadense*), wild sarsaparilla (*Aralia nudicaulis*), wood-sorrel (*Oxalis montana*), and goldthread (*Coptis groenlandica*). Certain deciduous shrubs, including speckled alder (*Alnus rugosa*) and witherod (*Viburnum cassinoides*), were important constituents of the understory in partially-opened, wet black spruce forest, but were of minor importance elsewhere. Interrupted fern (*Osmunda claytoniana*) was often the most conspicuous herbaceous species in the wet areas.

The characteristic breeding birds of the spruce-fir forest were:

Primary. Olive-backed thrush (*Hylocichla ustulata*), magnolia warbler (*Dendroica magnolia*), Cape May warbler (*Dendroica tigrina*), myrtle warbler (*Dendroica coronata*), bay-breasted warbler (*Dendroica castanea*), white-throated sparrow (*Zonotrichia albicollis*).

Secondary. Yellow-bellied flycatcher (*Empidonax flaviventris*), American crow (*Corvus brachyrhynchos*), black-capped chickadee (*Parus atricapillus*), brown-capped chickadee (*Parus hudsonicus*), red-breasted nuthatch (*Sitta canadensis*), winter wren (*Troglodytes troglodytes*), American robin (*Turdus migratorius*), hermit thrush (*Hylocichla guttata*), golden-crowned kinglet (*Regulus satrapa*), ruby-crowned kinglet (*Regulus calendula*), cedar waxwing (*Bombycilla cedrorum*), solitary vireo (*Vireo solitarius*), Tennessee warbler (*Vermivora peregrina*), Nashville warbler (*Vermivora ruficapilla*), Blackburnian warbler (*Dendroica fusca*), purple finch (*Carpodacus purpureus*), slate-colored junco (*Junco hyemalis*).

Minor. Broad-winged hawk (*Buteo platypterus*), pigeon hawk (*Falco columbarius*), spruce grouse (*Canachites canadensis*), saw-whet owl (*Aegolius acadica*), yellow-shafted flicker (*Colaptes auratus*), pileated woodpecker (*Dryocopus pileatus*), hairy woodpecker (*Dendrocopos villosus*), arctic three-toed woodpecker (*Picoides arcticus*), olive-sided flycatcher (*Nuttallornis borealis*), Canada jay (*Perisoreus canadensis*), blue jay (*Cyanocitta cristata*), brown creeper (*Certhia familiaris*), parula warbler (*Parula americana*), black-throated green warbler (*Dendroica virens*), Canada warbler (*Wilsonia canadensis*), evening grosbeak (*Hesperiphona vespertina*), pine grosbeak (*Pinicola enucleator*), pine siskin (*Spinus pinus*), white-winged crossbill (*Loxia leucoptera*).

White-winged crossbills were observed in the area during June, 1950, by James B. Cope and M. Max Hensley. They were not recorded in 1949, however.

The breeding birds of the spruce-fir forests near Sturgeon Lake, Ontario (Kendeigh 1947), and northern Maine are remarkably similar, although the two areas are approximately 950 miles apart. The most common birds in the Ontario area were the Tennessee warbler, Cape May warbler, bay-breasted warbler, and white-throated sparrow, all of which were also common in northern Maine. In the Lake Umbagog region of western Maine (Griscom 1938), the species of breeding birds in the spruce-fir community are also practically the same as those found in Ontario and northern Maine. Here as elsewhere in the boreal spruce-fir forest region, the Tennessee warbler, Cape May warbler, and bay-breasted warbler were found to vary greatly in numbers, being abundant some years and rare or absent during others. Kendeigh (1947) sum-

marizes data from the literature which would indicate that the occurrence as well as the abundance of these three species can often be correlated with outbreaks or severity of spruce budworm infestations.

Only a few pairs of evening grosbeaks were observed and these were at the edge of or in the general vicinity of forest clearings. An adult female collected on June 25 had enlarged gonads and a well developed brood-patch. All recorded observations of this species in Maine during the summer have been made from 1945 to the present (Palmer 1949), which may indicate an eastward extension of the breeding range of this big finch coincident if not correlated with the extension of the outbreak of spruce budworms.

Many birds characteristic of the boreal spruce-fir forests of northern and western Maine and Ontario drop out or become rare in the spruce-fir or related forests farther to the south. These include the Arctic three-toed woodpecker, yellow-bellied flycatcher, Canada jay, brown-capped chickadee, ruby-crowned kinglet, Tennessee warbler, Cape May warbler, and bay-breasted warbler. The absence or rarity of these species is noticeable in the red and white spruce forest on the coast of Maine (Cadbury and Cruickshank 1941); in the red spruce forest of the central Appalachians in West Virginia (DeGarmo 1948; Stewart and Aldrich 1949); in the spruce-hemlock bog forest of western Maryland (Stewart and Robbins 1951); and in the white cedar-balsam fir forest of northern Lower Michigan (Kendeigh 1948). The breeding birds in these four last-mentioned communities show a marked similarity to each other. In species composition and population of predominant species they actually resemble the birds of the white pine–hemlock forest of Vermont (Smith 1946) and the hemlock forests of Maryland (Robbins 1949) and North Carolina (Odum 1947) much more closely than those of the boreal spruce-fir forests to the north. For this reason it would, perhaps, be better to consider these more southern spruce-fir and related forests as being distinct and characteristic communities of the hemlock-hardwood region rather than of the boreal spruce-fir region.

Scrub–black spruce bog

The greater part of several of the large bogs in the area were covered by an open growth of scrub or stunted coniferous trees. These trees, the larger of which range between 10 and 15 feet in height, were predominantly black spruce with occasional tamarack. The majority of the branches on most of the trees were dead and covered with a dark beard-like lichen which had the effect of causing the entire habitat to have a very eerie appearance. The ground was covered with a thick, spongy mat of sphagnum moss, some hummocks of which ranged up to 1½ feet in depth. Sedges (*Carex* sp.) were common and a fairly dense growth of the various bog heaths was present. Of these, Labrador-tea (*Ledum groenlandicum*) and bog-laurel (*Kalmia polifolia*) were the most abundant species, although bog-rosemary (*Andromeda glaucophyla*) and leatherleaf (*Chamaedaphne calyculata*) were quite common too. Other plants which occurred regularly in the area included cotton-grass (*Eriophorum* sp.), large cranberry (*Vaccinium macrocarpon*) and pitcher-plant (*Sarracenia purpurea*). The characteristic breeding birds in this habitat were:

Primary. Hermit thrush, palm warbler (*Dendroica palmarum*), slate-colored junco, white-throated sparrow, Lincoln's sparrow (*Melospiza lincolnii*).

Secondary. Nashville warbler, yellow-throat (*Geothlypis trichas*).

Minor. Yellow-shafted flicker, cedar waxwing, myrtle warbler, purple finch, Song sparrow (*Melospiza melodia*).

In species composition this type appeared to be the most boreal of any of the habitats studied. All of the birds present are characteristic of the boreal spruce-fir forest region.

Alder bog shrub

Speckled alder was the predominant species in bog shrub communities located along many of the streams and in low places on the lake margins. Usually shrub willows (*Salix* sp.) were associated with the alder and there were frequently dead snags present as well as scattered trees of black ash (*Fraxinus nigra*), white cedar, and tamarack. Ordinarily there was also present a rank growth of herbaceous vegetation, consisting of sedges, grasses, and occasional common cattail (*Typha latifolia*). The characteristic birds of this habitat were:

Primary. Northern water-thrush (*Seiurus noveboracensis*), yellow-throat, red-wing (*Agelaius phoeniceus*), swamp sparrow (*Melospiza georgiana*).

Secondary and Minor. American bittern (*Botaurus lentiginosus*), Traill's flycatcher (*Empidonax traillii*), tree swallow (*Iridoprocne bicolor*), catbird (*Dumetella carolinensis*), veery (*Hylocichla fuscescens*), Wilson's warbler (*Wilsonia pusilla*).

It is of interest to note that all of the listed species with the exception of the Wilson's warbler are found in relict bog shrub communities in northeastern Ohio (Aldrich 1943).

White cedar–tamarack–black ash bog forest

Wooded bogs were found along many of the streams in the area. The canopy in this habitat was generally partly open and consisted principally of white cedar, tamarack, and black ash. Occasional balsam fir and black spruce were present, while speckled alder and willow were ordinarily common in the understory. The characteristic breeding birds in this habitat were:

Primary. Veery, northern water-thrush.

Secondary. Least flycatcher (*Empidonax minimus*), black-capped chickadee, black and white warbler (*Mniotilta varia*), parula warbler, magnolia warbler, Canada warbler.

Minor. American woodcock (*Philohela minor*), Arctic three-toed woodpecker, cedar waxwing, Tennessee warbler, Nashville warbler, Blackburnian warbler, yellow-throat, American redstart (*Setophaga ruticilla*), white-throated sparrow.

Conspicuous differences may be noted between this list and that for the tamarack–red maple–yellow birch relict bog forest of northeastern Ohio (Aldrich 1943), although the two primary species of the northern Maine area were also important in the Ohio bog communities.

Yellow birch–beech–sugar maple forest

Northern hardwoods were found on top of many of the hills and ridges. Practically all of these areas had been partially cut over resulting in an uneven growth of the overstory and the frequent occurrence of small brushy forest openings. The predominant trees in the overstory were yellow birch, beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*), while associated with them in lesser numbers were scattered balsam fir, red spruce, white spruce, hemlock (*Tsuga canadensis*), and red maple. A serious infestation of a species of insect which feeds in the cambium layers of birches had killed many of the large yellow birches leaving many dead snags in the forest. These were ideal nesting sites for woodpeckers, chickadees and nuthatches. In the understory ironwood (*Ostrya virginiana*), mountain maple, moosewood (*Acer pennsylvanicum*), red-berried elder (*Sambucus pubens*), beaked hazelnut (*Corylus cornuta*), and hobblebush (*Viburnum alnifolium*) were commonly associated with young trees and saplings of the overstory species. The characteristic breeding birds were:

Primary. Red-eyed vireo (*Vireo olivaceus*), black-throated blue warbler (*Dendroica caerulescens*), Blackburnian warbler, chestnut-sided warbler (*Dendroica pensylvanica*), oven-bird (*Seiurus aurocapillus*).

Secondary. Ruffed grouse (*Bonasa umbellus*), yellow-bellied sapsucker (*Sphyrapicus varius*), hairy woodspecker, downy woodpecker (*Dendrocopos pubescens*), Eastern wood pewee (*Contopus virens*), black-capped chickadee, American robin, hermit thrush, olive-backed thrush, parula warbler, magnolia warbler, black-throated green warbler, mourning warbler (*Oporornis philadelphia*), American redstart, rose-breasted grosbeak (*Pheucticus ludovicianus*), purple finch, slate-colored junco, white-throated sparrow.

Minor. Broad-winged hawk, black-billed cuckoo (*Coccyzus erythropthalmus*), whip-poor-will (*Caprimulgus vociferus*), ruby-throated hummingbird (*Archilochus colubris*), yellow-shafted flicker, pileated woodpecker, blue jay, American crow, white-breasted nuthatch (*Sitta carolinensis*), winter wren, cedar waxwing, Nashville warbler, myrtle warbler, Canada warbler, scarlet tanager (*Piranga olivacea*).

Many forest areas were actually intermediate between the yellow birch–beech–sugar maple type and the boreal spruce-fir type. In these areas, birds characteristic of both types were present.

The more common birds in the typical yellow birch–beech–sugar maple community were quite similar to those of a "Partially Cut-over Northern Hardwood Slope" near New Hampton, New Hampshire (Wallace 1948), the "Beech-Maple-Pine Forest" of northern Lower Michigan (Kendeigh 1948), and of a "Young Deciduous Growth" area between 4,100 and 4,200 feet elevation on Shavers Mountain, Monongahela National Forest, West Virginia (Stewart and Aldrich 1949). All of

these communities are characteristic of the hemlock-hardwood region.

Aspen forest

Stands of aspen usually developed on well-drained areas that had been burned over. They are eventually replaced either by spruce-fir or yellow birch–beech–sugar maple forests. Brushy openings were common in most of these stands, due to windfall, plant disease, or other causes. Quaking aspen was the predominant tree in the overstory, while associated with it as secondary species were white birch and pin cherry (*Prunus pensylvanica*). On moist sites, balsam-poplar (*Populus balsamifera*) and willow were common. Many of the large white birch were dead or dying from the ravages of the insect infestation so deadly to birches mentioned above. Patches of spruce and fir occurred regularly in the understory as well as various deciduous shrubs, including beaked hazelnut and mountain-ash (*Pyrus americana*). The characteristic breeding birds were:

Primary. Red-eyed vireo, Nashville warbler, American redstart.

Secondary. Ruffed grouse, black-capped chickadee, American robin, hermit thrush, olive-backed thrush, magnolia warbler, chestnut-sided warbler, oven-bird, mourning warbler, white-throated sparrow.

Minor. Yellow-shafted flicker, yellow-bellied sapsucker, hairy woodpecker, downy woodpecker, cedar waxwing, Philadelphia vireo (*Vireo philadelphia*), slate-colored junco.

A resemblance in species composition, although a difference in comparative abundance of birds, is noted between this and the yellow birch–beech–sugar maple forest. This is probably a reflection of the similarity in life form of the two communities.

Field border and wood margin

Certain birds were found to be especially characteristic of the brushy and wooded borders of agricultural fields, occurring either in wood-margin types between forests and fields or in hedgerows. The plants in these border habitats consisted of a considerable variety of species, the more important of which were: balsam poplar, quaking aspen, white birch, pin-cherry, choke cherry (*Prunus virginiana*), mountain-ash, box-elder (*Acer negundo*), red maple, mountain maple, and red-berried elder. A few of the birds characteristic of this habitat were also found along roadsides and in grassy clearings within the forests. The characteristic breeding birds were:

Primary. Song sparrow.

Secondary. Eastern kingbird (*Tyrannus tyrannus*), tree swallow, American robin, yellow warbler (*Dendroica petechia*), purple grackle (*Quiscalus quiscula*), American goldfinch (*Spinus tristis*), chipping sparrow (*Spizella passerina*).

Minor. Sparrow hawk (*Falco sparverius*), catbird, cedar waxwing, brown-headed cowbird (*Molothrus ater*).

It is noticeable that all of these species, like those of the next habitat, are very wide-ranging geographically and much less typically boreal than birds of forest and bog scrub habitats.

Agricultural field and sedge-meadow

Potatoes and occasionally other crops were grown in the agricultural fields. The savannah sparrow was the predominant breeding bird in most of these fields while horned larks (*Otocoris alpestris*) and vesper sparrows (*Poœcetes gramineus*) were common locally and there were a few killdeer (*Oxyechus vociferus*) present.

Sedge-meadows were found in some of the more open bogs and also occurred as swales on wet spots within agricultural fields. The vegetation of most of these meadows was composed of deep mats of sphagnum and other mosses partially covered with fairly dense growths of sedge and grasses. As far as could be determined, the savannah sparrow (*Passerculus sandwichensis*) was the only breeding bird of this habitat.

Lakes and streams

Occasional water birds were observed on Cross Lake, Mud Lake, and Long Lake, and along some of the larger streams. Species which appeared to be restricted to the lakes included the common loon (*Gavia immer*), ring-necked duck (*Aythya collaris*), American goldeneye (*Bucephala clangula*), American merganser (*Mergus merganser*), bald eagle (*Haliaeetus leucocephalus*), and osprey (*Pandion haliaetus*). Other birds found frequenting the lake margins and larger streams were the great blue heron (*Ardea herodias*), black-crowned night heron (*Nycticorax nycticorax*), black duck (*Anas rubripes*), spotted sandpiper (*Actitis macularia*), and belted kingfisher (*Megaceryle alcyon*). A few herring gulls (*Larus argentatus*) and at least one double-crested cormorant (*Phalacrocorax auritus*) were also seen on the lakes, but these were believed to represent non-breeding birds.

Miscellaneous

The barn swallow (*Hirundo rustica*), common starling (*Sturnus vulgaris*) and English

sparrow (*Passer domesticus*) were characteristic of barnyards and those areas adjacent to them. Bank swallows (*Riparia riparia*) were locally common in the vicinity of the gravel or clay pits located in the open agricultural areas. A few Wilson's snipe (*Capella gallinago*) were present in the vicinity of wet pastured lands. Common nighthawks (*Chordeiles minor*) and chimney swifts (*Chaetura pelagica*) were occasionally observed over practically all of the various land habitats.

Occurrence Rate of Woodland Birds

In 1951, on June 19–20, an attempt was made to obtain supplementary information on the occurrence rate and general distribution of woodland birds. Five-minute stops were made at ¼ mile intervals along the roads that pass through the wooded areas and every species of bird that was observed was recorded for each station. The observations were made between 5:30 A.M. and 10:00 A.M. along two roads, one extending from Cross Lake to Lake Madawaska and the other extending from Cross Lake to the village of Sinclair. These roads pass through various types of woodland habitats which represent different stages in the natural plant succession. A total of 50 stations was made in the extensive lowland wooded flats (elevation about 600 feet) and 17 stations in the wooded areas of the low-lying ridges which rise some 200 feet above the lowlands. The occurrence rate for each species on the lowland flats and on the ridges is indicated by the percentage of occurrence taken to the nearest 15 per cent (Table I). Occurrence rates of 7 per cent or less are indicated by plus (+) signs. These percentages are based on the number of stations at which each species was recorded.

Marked differences in the occurrence rates of the various species are apparent. Certain species, found to be widespread (occurrence rate of 45 per cent or more) in both lowland and ridges, were represented by the winter wren, American robin, red-eyed vireo, parula warbler, magnolia warbler, slate-colored junco and white-throated sparrow. A few species that were found to have high occurrence rates in the lowland areas, but which were of less importance on the ridges, included the olive-backed thrush, Nashville warbler, Cape May warbler, myrtle warbler and bay-breasted warbler. Still others that were of major importance in the upland areas, but which were relatively unimportant in the lowlands, included the black-throated blue warbler, Blackburnian warbler, chestnut-sided warbler and ovenbird.

General Population Studies of Forest Birds

In 1949, the populations of territorial males were determined in two tracts of spruce-fir forest by using the spot-mapping method (see Audubon Field Notes, 1950, Vol. IV, No. 2, p. 185). Most of the census trips were taken on these areas between 6:00 A.M. and 10:30 A.M. A few trips were made on each area in the evening for the determination of thrush populations which are more vocal at that time. Each census trip represented one complete cruise of the study area. Twenty-five census trips totaling 55 man-hours were conducted on a square (440 × 440 yards) 40-acre tract of spruce-fir forest during the period June 6 to 14, and 15 census trips involving 27 man-hours were made on a rectangular (440 × 330 yards) 30-acre tract of spruce-fir forest during the period June 9 to 11. The vegetation in these two tracts was similar, including sections with partially opened canopy as well as sections with a closed canopy. The predominant tree species in the overstory were black spruce and balsam fir. Populations of territorial males for these two tracts are shown in Table I. The first figure after each species represents the population density (number of males per 100 acres, taken to the nearest whole number); while the figures in parentheses represent the actual number of males in the study tracts (taken to the nearest half).

The number of territorial males in a 35-acre tract of the ridge mixed northern hardwood–spruce–fir forest was deter-

mined by Cope and Hensley (1951) during June, 1950. This area was located within the region covered by this report and it is interesting to compare its bird population with the population of the two spruce-fir areas (see Table I). The total population density of the ridge forest is noticeably less, and as would be expected the species composition is also quite different. Certain species, such as the red-eyed vireo, parula warbler, black-throated blue warbler, black-throated green warbler and oven-bird, were found to be quite numerous in the ridge forest but were of minor importance in the lowland spruce-fir areas. On the other hand several boreal species that were prominent in portions of the spruce-fir tracts were rare or absent in the ridge area. These included the yellow-bellied flycatcher, brown-capped chickadee, ruby-crowned kinglet, Tennessee warbler, Cape May warbler, myrtle warbler and bay-breasted warbler. Differences in the densities of the birds within the two spruce-fir tracts can be largely attributed to differences in the prevalence of the required habitat niches of the various species.

At the time of our studies the spruce-fir forest was undergoing a moderate infestation of the spruce budworm. Since this would have the effect of greatly increasing the available food supply, some of the insectivorous birds may have been considerably more common than they would be in a similar forest habitat without such an infestation. Robert T. Mitchell, in an unpublished manuscript

TABLE I. *General population studies of woodland birds*

	Occurrence rate, %		Population densities		
			Spruce-fir forest		N. hardwood, spruce-fir 35 acres 1950
	Lowland 50 stations 1951	Ridges 17 stations 1951	40 acres 1949	30 acres 1949	
Broad-winged hawk	+	+	–	–	–
Spruce grouse	–	–	–	+	–
Ruffed grouse	–	–	+	–	–
Yellow-shafted flicker	15	15	3 (1)	2 (.5)	–
Pileated woodpecker	+	30	–	+	–
Yellow-bellied sapsucker	15	15	–	+	3 (1)
Hairy woodpecker	+	30	–	3 (1)	1 (.5)
Downy woodpecker	–	–	–	+	–
Arctic three-toed woodpecker	+	15	+	+	–
Yellow-bellied flycatcher	30	–	10 (4)	–	–
Least flycatcher	15	15	–	–	–
Eastern wood pewee	–	+	–	+	6 (2)
Olive-sided flycatcher	15	–	–	–	–
Canada jay	15	+	+	–	–
Blue jay	15	15	4 (1.5)	2 (.5)	3 (1)
American crow	15	+	+	+	–
Black-capped chickadee	+	15	5 (2)	3 (1)	9 (3)
Brown-capped chickadee	15	+	6 (2.5)	10 (3)	+
White-breasted nuthatch	–	+	–	+	–
Red-breasted nuthatch	15	15	9 (3.5)	8 (2.5)	–
Brown creeper	–	–	+	–	–
Winter wren	45	45	5 (2)	3 (1)	–
Catbird	+	–	–	–	–
American robin	60	45	5 (2)	8 (2.5)	1 (.5)
Hermit thrush	15	15	5 (2)	3 (1)	1 (.5)
Olive-backed thrush	75	30	19 (7.5)	23 (7)	14 (5)
Veery	+	–	–	–	–
Golden-crowned kinglet	15	–	10 (4)	13 (4)	–
Ruby-crowned kinglet	30	–	5 (2)	10 (3)	–
Cedar waxwing	+	+	–	–	–
Solitary vireo	15	–	8 (3)	10 (3)	3 (1)
Red-eyed vireo	60	90	4 (1.5)	7 (2)	54 (19)

TABLE I—*Continued*

	Occurrence rate, %		Population densities		
			Spruce-fir forest		N. hardwood, spruce-fir 35 acres 1950
	Lowland 50 stations 1951	Ridges 17 stations 1951	40 acres 1949	30 acres 1949	
Black and white warbler	+	+	—	—	—
Tennessee warbler	15	—	8 (3)	10 (3)	—
Nashville warbler	45	15	10 (4)	5 (1.5)	—
Parula warbler	45	45	3 (1)	7 (2)	26 (9)
Magnolia warbler	75	60	60 (24)	50 (15)	10 (3.5)
Cape May warbler	45	15	30 (12)	27 (8)	—
Black-throated blue warbler	+	45	—	3 (1)	29 (10)
Myrtle warbler	45	30	21 (8.5)	20 (6)	+
Black-throated green warbler	—	30	—	—	23 (8)
Blackburnian warbler	30	75	23 (9)	20 (6)	30 (10.5)
Chestnut-sided warbler	30	60	+	—	+
Bay-breasted warbler	60	—	88 (35)	50 (15)	—
Oven-bird	15	75	4 (1.5)	+	23 (8)
Northern water-thrush	15	—	—	—	—
Mourning warbler	15	+	—	—	—
Yellow-throat	15	15	—	—	—
Wilson's warbler	+	—	—	—	—
Canada warbler	15	15	1 (.5)	+	—
American redstart	15	15	—	—	3 (1)
Red-wing	+	—	—	—	—
Purple grackle	+	—	—	+	—
Scarlet tanager	+	—	—	—	3 (1)
Rose-breasted grosbeak	+	30	—	—	—
Purple finch	15	30	6 (2.5)	3 (1)	+
Pine grosbeak	15	—	—	3 (1)	—
Pine siskin	+	—	—	3 (1)	—
American goldfinch	+	—	—	—	—
Slate-colored junco	45	60	13 (5)	8 (2.5)	—
White-throated sparrow	90	60	9 (3.5)	7 (2)	—
Swamp sparrow	+	—	—	—	—
Song sparrow	15	—	—	—	—
Total population			370 (148)	323 (97)	241 (84.5)

in the files of the U. S. Fish and Wildlife Service, gives abundant evidence that the birds collected in the present study had been feeding heavily on budworm larvae and pupae. Kendeigh (1947) concluded that there was a correlation between spruce budworm outbreaks and abundance of warblers. He gave evidence from the literature that outbreaks of these insects in the past had been accompanied by noted increases in warblers during migration. As further substantiation of this it might be noted that there was a conspicuous increase of the Cape May and bay-breasted warblers in migration along the Atlantic seaboard in 1949 and 1950. This was recorded for the fall migration of 1949 by Griscom (1950) and the spring migration of 1950 by Nichols (1950) and Potter and Murray (1950). These species are normally rare migrants in this area. A progress report "Spruce Budworm Surveys in Maine in 1949" by the Maine Forest Service and the U. S. Bureau of Entomology and Plant Quarantine, and also the Annual Reports of the Forest Insect Survey, Department of Agriculture, Canada, for 1948 and 1949, show a very marked rise in budworm populations in Maine and adjoining Maritime Provinces of Canada in 1948 and 1949. A correlation seems to exist between abundance of spruce budworms and Cape May and bay-breasted warblers during 1949

and 1950 in the breeding season in northern Maine as well as along the Atlantic seaboard in migration.

Population of Spruce-Fir Subtypes and Related Habitats

Due to the complex nature of the spruce-fir communities and the irregular occurrence of many of the required niches of the various species that inhabit them, the total populations and species composition of birds were found to vary considerably. The populations of territorial males in the 40-acre and 30-acre spruce-fir tracts were 148 (370 males per 100 acres) and 97 (323 males per 100 acres), respectively, while the population of various segregate subtypes were found to range from 221 to 430 males per 100 acres. This diversity of species composition and abundance in different types of spruce-fir forest validates the conclusions of Osborn and Kellogg (1943) that there are "direct correlations between the frequency of certain species and particular habitat elements of importance to them." "The total of all habitat elements is not so significant in determining total wildlife abundance as the presence or absence of certain critical elements for each particular species."

The numbers of territorial males in various spruce-fir subtypes as well as in other closely related habitats were determined by using the spot-mapping method. Analyses of these subtypes are based on several study areas which are described as follows:

Mature spruce-fir forest with closed canopy. 32½ acres of this type were censused in 1949

Table II. *Population of spruce-fir forest sub-types and related habitats*

	Spruce-fir forest				Scrub black spruce bog	Bog shrub
	Mature stand, closed canopy	Open mature stand, dense understory	Young stand	Open mature stand, without brush understory		
Acreage	32½	16½	28½	21	40	18
Year	1949	1949	1951	1949	1949	1949
Species—						
Pigeon hawk			+			
Spruce grouse	+					
Ruffed grouse		+				
Yellow-shafted flicker		3 (.5)	+	2 (.5)	1 (.5)	3 (.5)
Pileated woodpecker	+		+			
Yellow-bellied sapsucker				+		
Hairy woodpecker		+		+		3 (.5)
Downy woodpecker						+
Arctic three-toed woodpecker		+				3 (.5)
Yellow-bellied flycatcher	5 (1.5)	12 (2)	12 (3.5)	+		3 (.5)
Least flycatcher			4 (1)	+		+
Eastern wood pewee						3 (.5)
Olive-sided flycatcher			+	+		
Canada jay	+	+				
Blue jay	2 (.5)	6 (1)				
American crow	+	+	+	+		
Black-capped chickadee	5 (1.5)	3 (.5)	2 (.5)	2 (.5)		3 (.5)
Brown-capped chickadee	6 (2)	6 (1)	5 (1.5)	2 (.5)		
Red-breasted nuthatch	12 (4)	9 (1.5)	4 (1)	7 (1.5)		+
Brown creeper	+					+
Winter wren	2 (.5)	9 (1.5)	4 (1)	5 (1)		11 (2)
American robin	5 (1.5)	9 (1.5)	16 (4.5)			11 (2)
Hermit thrush	6 (2)	3 (.5)	+	17 (3.5)	19 (7.5)	
Olive-backed thrush	18 (6)	24 (4)	21 (6)	14 (3)		14 (2.5)

TABLE II—*Continued*

	Spruce-fir forest				Scrub black spruce bog	Bog shrub
	Mature stand, closed canopy	Open mature stand, dense understory	Young stand	Open mature stand, without brush understory		
Golden-crowned kinglet	18 (6)	3 (.5)		10 (2)		
Ruby-crowned kinglet	12 (4)	3 (.5)	3 (1)	12 (2.5)		
Cedar waxwing				+	3 (1)	
Solitary vireo	9 (3)	12 (2)	2 (.5)	12 (2.5)		
Red-eyed vireo			14 (4)			
Black and white warbler			+			11 (2)
Tennessee warbler	9 (3)	9 (1.5)	+	10 (2)		6 (1)
Nashville warbler		15 (2.5)	19 (5.5)	10 (2)	3 (1)	8 (1.5)
Parula warbler		6 (1)	4 (1)			8 (1.5)
Magnolia warbler	23 (7.5)	100 (16.5)	32 (9)	7 (1.5)		33 (6)
Cape May warbler	43 (14)	12 (2)	4 (1)	+		
Myrtle warbler	34 (11)	9 (1.5)	26 (7.5)	10 (2)	1 (.5)	3 (.5)
Blackburnian warbler	12 (4)	36 (6)	2 (.5)	5 (1)		3 (.5)
Chestnut-sided warbler						8 (1.5)
Bay-breasted warbler	71 (23)	106 (17.5)	95 (27)	43 (9)		6 (1)
Palm warbler					24 (9.5)	
Oven-bird			2 (.5)	+		
Northern water-thrush			12 (3.5)			28 (5)
Mourning warbler				+		
Yellow-throat					4 (1.5)	19 (3.5)
Wilson's warbler						6 (1)
Canada warbler		3 (.5)				6 (1)
American redstart			4 (1)			6 (1)
Purple finch	6 (2)	6 (1)	7 (2)	2 (.5)	3 (1)	3 (.5)
Pine grosbeak	3 (1)		4 (1)			
Pine siskin	+					
Slate-colored junco	11 (3.5)	12 (2)	9 (2.5)	14 (3)	13 (5)	3 (.5)
White-throated sparrow	6 (2)	12 (2)	14 (4)	43 (9)	25 (10)	61 (11)
Lincoln's sparrow					15 (6)	
Song sparrow					+	6 (1)
Total	318 (103.5)	430 (71)	318 (90.5)	226 (47.5)	108 (43.5)	292 (52.5)

including 19½ acres and 13 acres respectively from the 40-acre and 30-acre tracts of spruce-fir forest that were previously described. Balsam fir and black spruce were the primary dominant trees in both areas. The majority of the trees ranged between 40 feet and 60 feet in height. Understory woody plants were either sparsely represented or absent.

Open cut-over spruce-fir forest with dense coniferous understory. 16½ acres of this type were censused in 1949 including 14½ acres from the 40-acre tract of spruce-fir forest and 2 acres from the 30-acre tract. Both the open overstory and understory were composed primarily of balsam fir and black spruce.

Dense stand of young spruce-fir forest. A rectangular (660 × 208 yards), 28½-acre tract of this type was censused by Stewart and Webster (1951) during the period June 14–20, 1951. The stand consisted of "young coniferous trees averaging between 20 and 25 ft. in height with scattered deciduous trees averaging between 25 and 30 ft. in height. Analysis of tree composition based on transect 1980 ft. long and 10 ft. wide (all trees over 6 inches in diameter, D. B. H., counted): Black Spruce, 40%; Balsam Fir, 33%; Quaking Aspen (*Populus tremuloides*), 25%; White Birch (*Betula papyrifera*), 2%." Eight census trips were made on the area totaling 20 man-hours.

Open cut-over black spruce stand without woody understory. A square, 21-acre tract of open, selectively lumbered black spruce, containing very little underbrush, but with a well-developed lush, herbaceous layer. Standing trees averaged about 60 feet in height. Nine census trips were made on this area, involving about 10 man-hours, during the period June 24–27, 1949.

Scrub black spruce bog. A square, 40-acre tract, which was remarkably uniform throughout and was surrounded on all sides by extensive areas of the same habitat. The description of the scrub black spruce bog habitat type was given above under Biotic Communities and applies equally well to this study area. This is

believed to be the first time that a bird population study has been made in this type of habitat. A total of 13 census trips, involving about 17 man-hours, were conducted on the area during the period June 20–27, 1949.

Bog shrub. An 18-acre strip (792 × 110 yards) of alder bog mixed with saplings of deciduous and coniferous trees. The area was actually intermediate in many respects between the typical alder bog type and brushy cut-over spruce-fir forest. Seven census trips were conducted on the area involving about 5 man-hours on June 29, 1949.

The bird populations of these spruce-fir subtypes and related habitats are listed in Table II. The first figure in each column following a species represents the number of territorial males per 100 acres of habitat, while the figure in parentheses is the number of males or territories (taken to the nearest half) in the study area. A plus (+) sign is used for a species that is present, when the number of males or territories in a study area was less than ¼.

Occurrence of the habitat niches required by the various breeding species in the spruce-fir and related habitats was extremely variable and this was reflected in a differentiation in populations of birds from one area to another. Forest stands with a closed canopy usually had a comparatively high population of the "true" forest birds while the forest-edge species were rare or absent. The more common birds in closed forest type included the brown-capped chickadee, red-breasted nuthatch, golden-crowned kinglet, ruby-crowned kinglet, Cape May warbler, myrtle warbler, and bay-breasted warbler. Certain species appeared to be dependent on a coniferous brush layer which could occur as an understory in forests with a closed canopy, as a forest-edge brush layer, or as a dense thicket in recently cut-over areas. Birds that were largely restricted to these situations included the yellow-bellied flycatcher, winter wren, olive-backed thrush, magnolia warbler, and pine grosbeak. Still other species apparently required wooded edge or openings with a well-developed herbaceous layer. These included the robin, hermit thrush, Nashville warbler, purple finch, slate-colored junco, and white-throated sparrow. The Tennessee warbler, northern water-thrush and Arctic three-toed woodpecker were most common in wet forest types that had been partially opened by selective lumbering. Large sections of the spruce-fir forest had been selectively lumbered, resulting in fairly open stands of trees. In these areas the birds dependent on forest-edge niches predominated while the closed-forest birds were comparatively uncommon. A few species such as the bay-breasted warbler, myrtle warbler, and Blackburnian warbler occurred regularly in both forest and forest-edge types. Two species, the palm warbler and Lincoln's sparrow, were restricted to the scrub black spruce bogs, while the Wilson's warbler was found to occur only in the bog shrub.

The ecological relationship of certain species of wood warblers of the genus *Dendroica* is of particular interest. Study of the habitat favored by the closely related myrtle, bay-breasted, Cape May, and Blackburnian warblers, which we found to be four of the most abundant species in the spruce-fir forests, revealed only slight differences in their niche requirements which overlapped greatly. All four species nest and feed in the forest canopy. Although considerable interspecific competition among these tree-top birds has been recorded by Kendeigh (1947), their regular occurrence together in the same habitats would seem to be contrary to the thesis propounded by Gause (1934) and elaborated upon by Lack (1944) that closely related species tend to occupy different niches when their ranges overlap. It is possible, however, that under normal conditions these species do not overlap to the extent that we found them. Conditions which exist during a spruce budworm outbreak, although they may last for several years, are obviously not normal and may account for a greater geographical range overlap and transgression of niches by closely related species than dur-

ing periods when no outbreak of insects exists. Lack (1946: 126) described cases of overlap of feeding niches in the case of temporary superabundance of food and suggested that the facts are reconcilable with Gause's thesis, because the foods in question are temporarily so much more abundant than the requirements of the consumers that the latter do not effectively compete with each other while eating them.

Summary

Ecological studies were made of bird populations in the vicinity of Cross Lake in extreme northern Maine. These studies indicate that this area lies within an overlapping belt (ecotone) between two major biotic regions, the boreal spruce-fir forest region and the hemlock-hardwood region. Elements of each of these are abundantly represented in the plant and bird life, with the boreal elements predominating on the lowlands, the hemlock-hardwood elements predominating on the ridge tops and intermediate conditions existing on the mesophytic slopes. Within this general breakdown of predominating regional elements, the distribution of characteristic birds of each community was largely governed by appropriate niche occurrence.

The breeding birds of the spruce-fir forests in northern Maine are remarkably similar in species composition and populations to those studied by Kendeigh in the spruce-fir forest near Sturgeon Lake, Ontario. A marked similarity is also noticeable with the birds of the Lake Umbagog region of western Maine (Griscom 1938). It would appear that these coniferous communities are all characteristic of the same biotic region, the boreal spruce-fir forest region. Farther south, however, in the Appalachians and adjoining areas, the birds of the spruce-fir and related communities were found to resemble the birds of the hemlock–white pine forests of the hemlock–hardwood region much more closely than those of the boreal forests.

Each major community in the area was characterized by a definite association of breeding birds. The major communities that were recognized are: boreal spruce-fir forest, occurring extensively on the lowlands; scrub black spruce bog, occurring on wet poorly drained bog areas; alder bog shrub, located along many of the streams and in low places on the lake margins; white cedar–tamarack–black ash bog forest, representing a successional stage in the hydrosere, following the alder bog shrub; yellow birch–beech–sugar maple forest, climax community on top of many of the hills and ridges; aspen forest, occurring on forested areas that had previously been burned over; field border and wood margin in agricultural areas; agricultural fields; sedge-meadows; lakes and streams.

Within most communities the distribution and occurrence of the required habitat niches of the various resident birds were not uniformly distributed but varied with each species. As a result of this variation, the total populations of all species varied considerably in each community. This was indicated in studies of the spruce-fir forests where the total population of different sub-types varied from 221 to 430 territorial males per 100 acres. The population densities in scrub black spruce bogs and alder bog shrub were 109 and 292 males per 100 acres, respectively.

An outbreak of spruce budworm produced a superabundance of highly desirable bird food which probably supported a larger-than-normal population of forest and marginal bird life. According to unpublished work by Robert T. Mitchell, practically all of the small land birds in the area ate these insects. It is conceivable that as a result of the plentiful supply of food, the number of species, as well as the number of individual birds, was increased over the number normal for the area studied as postulated for a budworm-infested area in Ontario by Kendeigh.

Several closely related warblers of the genus *Dendroica* were found to occur regularly together in the same spruce-fir

habitats and occupied similar if not identical niches. This would seem to be contrary to the idea proposed by Gause that closely related species tend to occupy different niches when their ranges overlap. As indicated by Lack, however, a superabundance of food, such as a spruce budworm infestation, might cause a marked reduction in competition between closely related species, so that they are enabled to occupy the same areas.

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TREE SPECIES OCCURRENCE AS INFLUENCED BY GEOLOGY AND SOIL ON AN OZARK NORTH SLOPE

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This study reports an attempt to relate the occurrence of tree species, hence forest types, to soils and surface rock formations in the Ozark Highland of northern Arkansas. The evidence corroborates informal field observations in the region, and suggests that many of the major variations in forest composition and forest site productivity may be explained by soil differences attributable to different parent rock materials. Similar observations have been reported for different rock formations and plant associations in various parts of the country (Owen 1858; Billings 1950; Berkman 1928; Morrow 1931; Cuyler 1931; Read 1950; and others). Lutz and Chandler (1946: 61) have stated: "Although there are many references in the literature to the relationship between surface geology and the distribution and growth of forest trees, detailed studies are less common. . . . The best examples [of such relationships] usually occur on relatively immature soils."

While the geographic occurrence of the broad zonal groups of soils is determined principally by climate and secondarily by vegetation, the nature of the parent material, in small regions of uniform climate, is probably more important than any other single factor in determining character and productivity of soils (Lutz and Chandler 1946). Because of the diversity of rocks and topographic conditions, and the fact that soils are residual, and because it is a small region of relatively uniform climate, the Ozark Highland provides ample opportunities for studying the influence of geology upon soil formation, and the influence of rocks and soils upon types of vegetation. Several climaxes of permanent, well-marked associations exist in the Ozarks, often contiguous to each other but having originated from different substrata. Steyermark (1940) states that these are not climatic climaxes, as argued by Weaver and Clements (1938), but owe their diversity to the different origin of the soils on which they grow.

GEOLOGY, SOIL, VEGETATION, AND CLIMATE

All rocks in the Ozark Highland of Arkansas are sedimentary and essentially horizontal. They form a broad, elevated dome which has been intricately dissected during and since Paleozoic time. Erosion has carved deep valleys through the uppermost rocks of the lower Pennsylvanian series down through the oldest rocks of the lower Ordovician. In consequence, surface outcrop of rocks is determined by thickness and resistance to weathering of the various strata, by topographic position, and by amount of dissection within the entire Highland.

The Highland is divided into three plateaus, the Salem, the Springfield, and the Boston Mountain, so called because of the concordance of summit levels within each. The plateaus are separated by steep escarpments easily recognized in the field and shown in Figure 1.

There are ten major rock formations in the north-central Arkansas Ozarks. These occur between 500 feet elevation on the White River to over 2,000 feet above sea level on the Boston Mountains. Local relief ranges from 100 to 800 feet, and often exposes two or more major rock formations of different composition on one hillside. Minor geologic formations are present, but are too thin or inconsistent in occurrence to be of importance in relating distribution of tree species to soil type areas. Some of the major formations contain two or more separate members. Although members may be present or absent

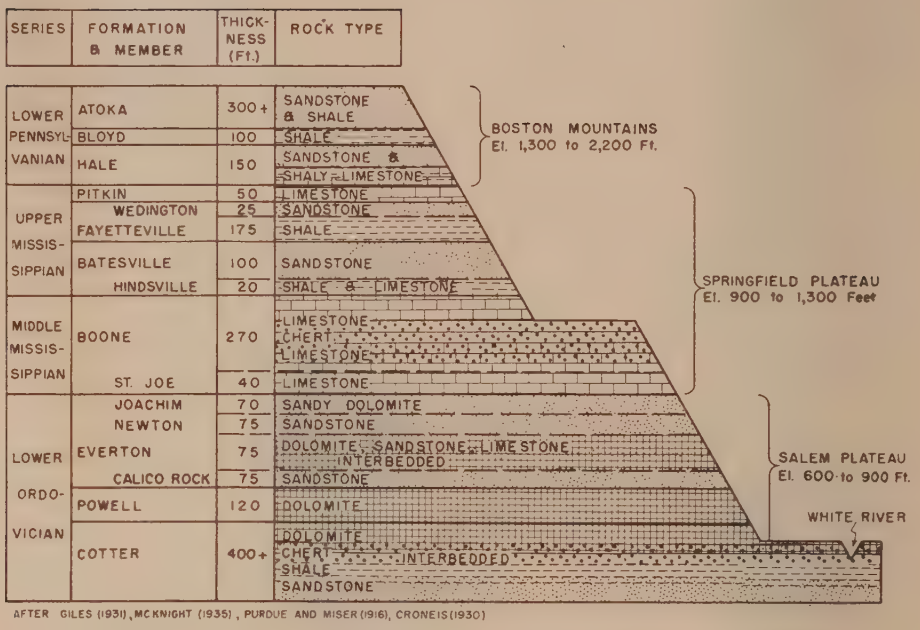

FIG. 1. Generalized column of geologic formations of the Ozark Highland of north-central Arkansas.

in a given locality, the major formations extend generally throughout the region.

Except for small areas of alluvium in stream bottoms and colluvium on the steeper slopes, the soils that mantle the present land surface have formed in place from the weathering of rocks. As a result, the soil types generally follow a pattern determined primarily by the outcrop of different rock formations.

Vegetation is the mesophytic forest made up of various associations owing their existence to differing soil, topographic, and slope conditions, and also to past history. Oaks, hickories, shortleaf pine, and eastern redcedar are the predominant forest trees.

Mean annual precipitation ranges from 35 inches in the northern Ozarks to over 50 inches in the south. Forty per cent of the precipitation is received in the spring, 33 per cent in summer and fall, and 27 per cent during the winter. Mean temperature in the northern Arkansas Ozarks ranges from 36° F in January to 75° F in July. The season between killing frosts averages 199 days per year.

Study Area

The study area is on the Koen Experimental Forest in Newton County, 17 miles south of Harrison, Arkansas, at latitude 36°03′ North, and longitude 93°10′ West (Fig. 2). It has not been disturbed by burning or cutting in the past 20 years, and grazing has been light to moderate. None of it has been cultivated.

Parts of both the Springfield and upper Salem Plateaus are represented in this area. The Boone formation forms the high ridges and upper slopes, while the Joachim and Newton members of the Everton form the lower slopes.

A fault extending from southwest to northeast made it possible to study the relation between tree species occurrence and soil types as derived from four different rock strata, all on the same aspect and slope. The study area has a north to

northeast aspect and a 20 to 30 per cent slope.

A small shallow ravine follows the fault line, but causes little change of slope or exposure. Rock strata on the southeast side of the fault have dropped about 300 feet from their position prior to faulting, thus bringing the Boone chert into lateral contact with both the St. Joe limestone and Newton sandstone. All strata have remained essentially horizontal.

The Boone formation averages 300 feet in thickness and consists of interbedded layers of gray, compact, coarsely-crystalline limestone and light-colored, compact chert. The basal St. Joe member (Fig. 1) is pure limestone. Above this member, the Boone is stratified both vertically and horizontally, so that some parts of the section are nearly all chert with little interbedded limestone, and other parts are pure limestone with but thin lenses of chert. Because the chert is very resistant to weathering in comparison to the limestone, it forms the bulk of residual rock material within the profile and on the soil surface. Soils derived from strata of the Boone where chert predominates are deep, freely permeable, light brown, cherty silt loams with frequently as much as 70 per cent of the volume throughout the profile occupied by chert fragments. Bedrock outcrops seldom occur on these areas.

In strata of the Boone formation where limestone predominates, bedrock outcrops are frequent. On the study area, this occurs on the slopes below the thick chert beds which form the ridges. In consequence, soils on these areas are derived from a mixture of materials. The surface foot of soil is a light brown cherty silt loam similar to the surface soil developed exclusively on chert, while the subsoil grades into a heavy reddish clay loam and finally to a plastic red clay over limestone bedrock.

The St. Joe member of the Boone formation averages 40 feet in thickness

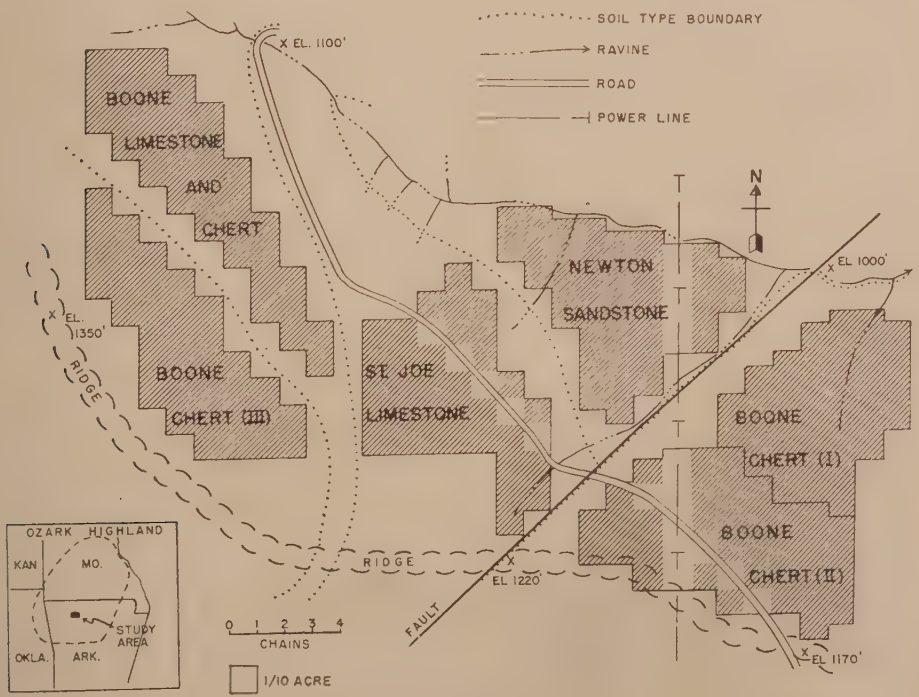

FIG. 2. The study area.

TABLE I. *Density and frequency of trees larger than 3.5 inches d.b.h. on six 3½-acre soil type areas of north to northeast aspect near a fault zone in Newton County, Arkansas*

Tree species		Rock formation from which soil is derived											
Scientific name[1]	Common name	St. Joe limestone		Boone limestone and chert		Boone chert (I)		Boone chert (II)		Boone chert (III)		Newton sandstone	
		D	F	D	F	D	F	D	F	D	F	D	F
Juniperus virginiana	Eastern redcedar	3.83	30	0.17	6	0.23	6	0.17	6	0.14	4	0.20	4
Quercus borealis	Northern red oak	2.11	27	3.54	32	.46	12	.49	11	.31	8	.51	11
Ulmus alata	Winged elm	1.03	23	1.03	18	.09	3	.86	13	.14	3	.40	9
Quercus muhlenbergii	Chinquapin oak	.94	19	.49	12					.09	3		
Carya ovata	Shagbark hickory	.94	17	.31	8	.03	1					.03	1
Fraxinus americana	White ash	.63	12	1.49	25	.03	1	.17	4			.11	3
Celtis occidentalis	Hackberry	.46	9										
Juglans nigra	Eastern black walnut	.31	9	.20	6					.06	2	.06	1
Diospyros virginiana	Common persimmon	.31	8	.03	1			.17	6	.03	1	.03	1
Acer saccharum	Sugar maple	.17	5	.03	1	.03	1					.06	2
Cercis canadensis	Eastern redbud	.17	5	.03	1	.03	1	.03	1	.03	1		
Pinus echinata	Shortleaf pine	.06	2					.06	2	.17	6	.17	4
Ulmus fulva	Slippery elm											.03	1
Ostrya virginiana	Eastern hophornbeam	.09	2					.06	2				
Prunus serotina	Black cherry							.03	1				
Robinia pseudoacacia	Black locust	.03	1	.06	2					.03	1		
Platanus occidentalis	American sycamore					.03	1	.11	4				
Quercus stellata	Post oak	.03	1					.17	3				
Liquidambar styraciflua	Sweetgum					.11	3	.11	2				
Morus rubra	Red mulberry					.11	4	.14	4	.03	1		
Acer rubrum	Red maple					.11	4	.09	2	.03	1	.23	7
Quercus falcata	Southern red oak					.14	5					.29	4
Sassafras albidum	Sassafras	.06	2	.11	4	.29	7	.89	16	.06	2	.20	4
Castanea ozarkensis	Ozark chinquapin					.60	17	.66	11	.57	10	1.03	16
Nyssa sylvatica	Blackgum					.83	17	.69	14	.40	7	1.14	24
Carya texana var. *arkansana*	Arkansas black hickory					.31	10	2.11	27	.09	2	.11	4
Carya tomentosa	Mockernut hickory			.57	14	.97	20	.17	5	1.40	24	.46	13
Cornus florida	Flowering dogwood	.11	3	.46	11	1.94	24	1.06	17	1.26	21	1.11	19
Quercus alba	White oak	.91	11	2.03	23	5.03	33	2.11	28	1.37	19	1.51	21
Quercus velutina	Black oak	.17	2	1.83	24	5.31	33	9.63	35	7.00	35	3.23	32
Av. number stems per quadrat (all species)		12.36		12.38		16.68		19.98		13.20		10.91	

Basis: Thirty-five 1/10-acre quadrats for each rock formation.
D = average number of stems per 1/10 acre quadrat. F = number of quadrats out of 35 having at least 1 representative of species.
[1] Nomenclature after: U. S. Forest Service. 1944. *Check list of the native and naturalized trees of the United States, including Alaska.* 325 pp. (Mimeographed.)

and consists of gray to pink coarsely-crystalline limestone which is chert-free. Soils are characteristically shallow, dark reddish-brown silty clays resting directly upon limestone slabs. Outcrops are abundant, and in some places probably cover over one-half of the surface.

The Newton member of the Everton formation averages 75 feet in thickness and consists of white to buff, massive, friable, saccharoidal sandstone. It frequently forms conspicuous bluffs. Soils vary from shallow, loamy sand overlying bedrock, particularly above bluffs and on convex slopes of ridges, to deep, brown, loamy sands on long slopes below bluffs. Bedrock outcrops are not common as on limestone areas, but sandstone "floaters," large chunks separated from bedrock, are abundant on the surface and within the soil profile.

Study Methods

In 1949, soon after it was established, the entire 800-acre Koen Experimental Forest was divided into one-tenth acre quadrats (66 feet square) and inventoried, quadrat by quadrat. The inventory was made by establishing a grid by means of string lines running north and south one chain apart and marked off at one-chain intervals. Inventory records include a physical description of the site and a tally, by species and size, of every tree larger than 3.5 inches in diameter at breast height (4½ feet above ground).

When it was decided to compile the data for the present study, six areas, each representing a single rock and soil type, were delineated on the map of the forest. Thirty-five quadrats were selected from each area. Quadrats including roads and power lines, and those overlapping soil type boundaries, were excluded. Three Boone chert areas were selected near the fault zone, but only one sample of each of the other soil type areas was available at this location.

Density of each species in each area was determined by totaling the number of stems and dividing by the number of

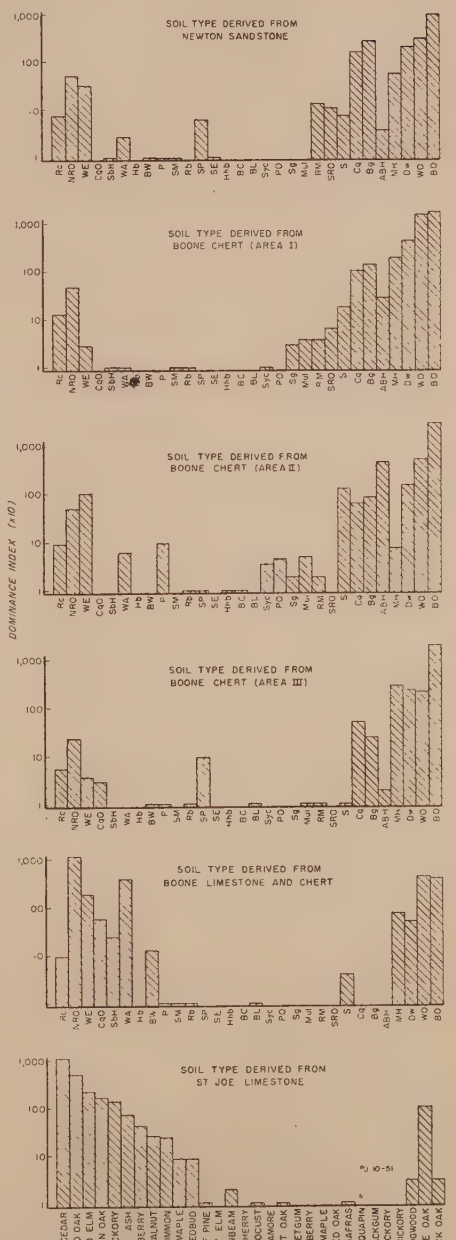

FIG. 3. Dominance indices for trees larger than 3.5 inches in diameter at breast height, on six 3½ acre areas of a north and northeast exposure in Newton County, Arkansas.

TABLE II. *Tree species ranked by dominance index and potential commercial importance on 4 soils from different parent materials*

Parent material	Ranked by observed dominance index	Ranked by potential commercial importance in forest management
Boone chert	1. Black oak 2. White oak 3. Flowering dogwood 4. Mockernut hickory 5. Blackgum	1. White oak 2. Black oak
Boone limestone with cherty surface soil	1. Northern red oak 2. White oak 3. Black oak 4. White ash 5. Winged elm	1. White oak 2. Northern red oak 3. White ash 4. Black oak
St. Joe limestone	1. Eastern redcedar 2. Northern red oak 3. Winged elm 4. Chinquapin oak 5. Shagbark hickory	1. Eastern redcedar
Newton sandstone	1. Black oak 2. White oak 3. Blackgum 4. Flowering dogwood 5. Ozark chinquapin	1. White oak 2. Black oak

quadrats in the area. Frequency of each species in each area was determined in this study by counting number of quadrats having at least one representative of the species (35 is thus the maximum possible frequency here). Dominance index for each species is the product of density times frequency (Turner 1936). In Figure 3, dominance indices are multiplied by ten.

RESULTS

Predominance of certain tree species and species groups according to surface rock formations and their derived soils is strikingly shown by Table I and Figure 3, where species are grouped so as to bring together those dominating on limestone, and those dominating on chert and sandstone.

The five predominant species, and those which by reason of growth and quality on these particular soils should be favored in forest management on similar sites, are summarized in Table II.

Black oak, white oak, flowering dogwood, sassafras, northern red oak, eastern redcedar, winged elm, and persimmon appear to be the most ubiquitous species. However, the first four of these appear less frequently and the last four more frequently on the St. Joe limestone than on the Boone chert and Newton sandstone soils.

Mockernut hickory, Arkansas black hickory, blackgum, Ozark chinquapin, and red maple are absent on the St. Joe limestone, but occur consistently on Boone chert and Newton sandstone soils. Chinquapin oak, shagbark hickory, white ash, hackberry, black walnut, redbud, and sugar maple occur rather consistently on St. Joe limestone, but are very limited and spotty on Boone chert and Newton sandstone soils.

Species dominance on the soil derived from Boone limestone and chert appears to be intermediate to the two extremes. Here, northern red oak, winged elm, chinquapin oak, shagbark hickory, white ash, and black walnut, so characteristic of the pure limestone soil, share dominance with the black oak, white oak, dogwood, and mockernut hickory of the cherty soil.

Species dominance on Newton sandstone soil is similar to that on Boone chert, except that blackgum and red maple are slightly more abundant on the sandy soil than on the cherty soil.

Other investigators have found that the leaf litter of species predominating on limestone soils usually contains more calcium than that of species which occur less frequently on such sites. Species whose leaf litter normally contains over two per cent calcium (dry-weight basis) include eastern redcedar, shagbark hickory, white ash, hackberry, black walnut, mockernut hickory, and dogwood (Lutz and Chandler 1946; Chandler 1939; Broadfoot and Pierre 1939). In this connection, it is interesting to note that five of the ten predominant species on the St. Joe and Boone limestone soils are those whose leaf litter normally contains more than two per cent calcium, whereas on the Boone chert and Newton sandstone soils only two of the ten predominants are in that category. No information is available on the calcium content of the litter of winged elm, chinquapin oak, and redbud, which are also common on the limestone soils included in the present study.

It cannot be stressed too strongly that these observations relate specifically to a north and northeast aspect. Numerous checks made in other areas of like parent material, aspect, and slope indicate essentially the same predominance of species or species groups according to the soil and rock types. On other aspects and slopes of Boone chert and Newton sandstone, different species may predominate and be better suited for management. On St. Joe limestone, however, aspect and slope do not seem to influence the species composition to any great extent, and the sole species to be favored in forest management is redcedar, regardless of the aspect or slope.

Discussion

Since climate and time, as factors of soil formation, have been essentially uniform throughout this region, it appears that the major differences in forest soils are a result of differences in parent rock materials, conditioned by topography and biological action. The physical and chemical makeup of different parent materials varies, and consequently the rate and effect of weathering differ according to the individual stratum and its topographic position. For example, soil on areas of dolomite evolves at a different rate from soil on areas of cherty limestone or sandstone. Furthermore, those soils on north slopes derived from cherty limestone differ from soils similarly derived but on south slopes.

Lutz and Chandler (1946) state that the differentiating effects of parent material are greatest in immature soils, which may be chemically unbalanced or deficient, especialy when derived from a single geological formation. Since most of the forest soils in this region are immature and are usually derived from a single rock formation, the nature of the parent material may be more important than is usually realized.

Thus there is ample theoretical justification, substaniated by results of this study and other informal observations, for using geologic information as a basis for forest site classification in the Ozarks. Given the geologic formation or portion thereof, and the topographic position, aspect, and slope, it may be possible to predict tree species occurrence, and to state the species or group of species that should be favored in management. Such prediction may prove especially useful in evaluating forest site potentialities when burning, cutting, grazing, or cultivation has altered existing species composition so that it is unrealiable as an indicator of site.

Summary

This study provides quantitative evidence of natural relationships between tree species occurrence and types of soil as derived from different surface geologic formations in the northern Arkansas Ozarks.

1. Study areas have a common north to northeast exposure of uniform slope, and each is wholly within a uniform soil condition. The areas have been undisturbed for 20 years.

2. All trees larger than 3.5 inches in d.b.h. were inventoried by $\frac{1}{10}$-acre quadrats, on six $3\frac{1}{2}$-acre areas representing four different soil and rock types.

3. Black oak, white oak, dogwood, blackgum, and mockernut hickory predominated on soils derived from both the Boone chert and the Newton sandstone.

4. Eastern redcedar, northern red oak, winged elm, chinquapin oak, and shagbark hickory predominated on soil derived from St. Joe limestone.

5. The predominant species on Boone limestone and chert included some that were dominant on St. Joe limestone and some that dominated on Boone chert.

6. Mockernut hickory, Arkansas black hickory, blackgum, Ozark chinquapin, and red maple were prevalent on cherty and sandy soil areas, but did not occur on the St. Joe limestone.

7. Chinquapin oak, shagbark hickory, white ash, black walnut, sugar maple, hackberry, and redbud were prevalent on the St. Joe limestone, but not on the cherty or sandy soils.

8. Of the tree species whose leaf litter contains relatively large amounts of calcium, a greater proportion occurred on the St. Joe and Boone limestone than on the Boone chert or Newton sandstone.

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PROCESSES CONTRIBUTING TO THE DECREASE OF COLIFORM BACTERIA IN A TIDAL ESTUARY[1]

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INTRODUCTION

It has long been known that coliform bacteria introduced into tidal waters disappear rapidly so that the numbers decrease from many thousands per ml. in the region where the water is practically fresh to very few, or none at all, where the water approaches a salinity characteristic of sea water. Many factors have been postulated to account for such pronounced decreases, but their relative importance has never been quantitatively assessed.

Dilution of the river water with sea water is important, but it is not sufficient to explain the enormous decreases that are observed. ZoBell (1936, 1946), Ketchum *et al.* (1949), and Vaccaro *et al.* (1950) have pointed out the importance of the bactericidal action of sea water. The zooplankton in the water remove organisms and particulate matter from the water which they filter, and Fuller (1937) and Harvey (1937) have evaluated the effective filtration rate. Weiss (1951) has studied the adsorption of *E. coli* on river and estuarine silts, and his results suggest that sedimentation may deposit many of the coliform bacteria on the bottom.

A quantitative evaluation of these various factors is possible only when the circulation and exchanges of the fresh and salt water in the estuary are known. With a knowledge of the circulation, direct calculation of the effect of dilution can be made, and the effects of bactericidal action and of predation by zooplankton can then be evaluated.

This paper presents an interpretation of observations made in the Raritan River, New Jersey. It is shown that the observed distribution of coliform bacteria within the tidal reaches of the Raritan River closely approximates the distribution to be expected as a result of the cumulative effects of the bactericidal action of sea water, predation by zooplankton and dilution.

DISTRIBUTION OF PROPERTIES

On June 26 and 27, 1949, surveys of the Raritan River were made, during

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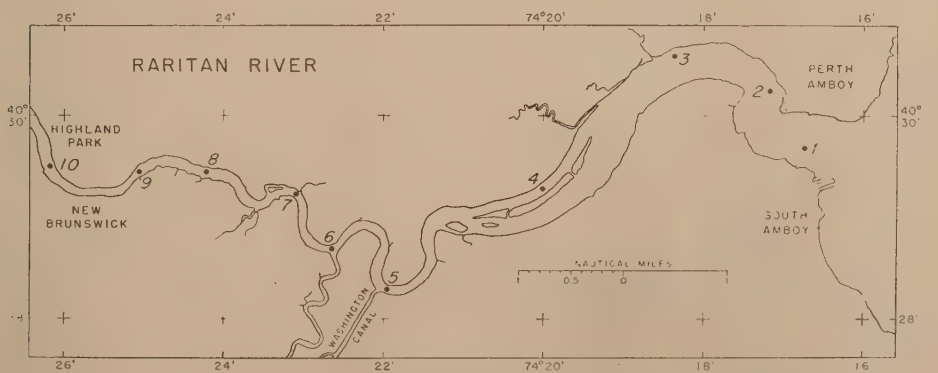

FIG. 1. Chart of Raritan River showing location of stations occupied during the survey.

which time eight stations were occupied within an hour of low tide, and ten stations were occupied within an hour of high tide. The location of these stations is shown in Figure 1.

The surface distribution of salinity and temperature was obtained using a salinity-temperature-depth recorder (Jacobson 1948). At each station a record of vertical distribution was obtained by lowering the measuring elements of this instrument to the bottom. Since the water in the river was generally stratified vertically, water samples and plankton tows were taken both above and below the halocline. Nansen bottle samples were analyzed for

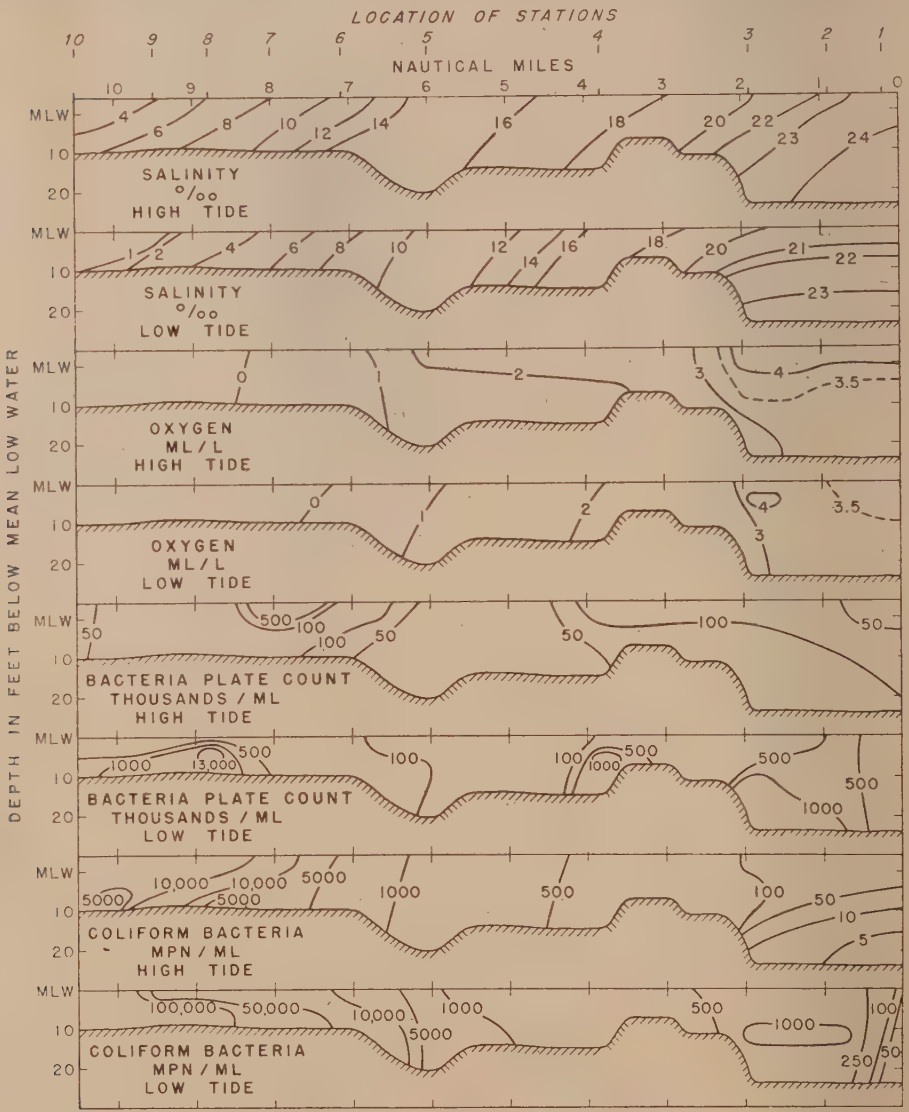
LOCATION OF STATIONS
NAUTICAL MILES
DEPTH IN FEET BELOW MEAN LOW WATER
SALINITY °/oo HIGH TIDE
SALINITY °/oo LOW TIDE
OXYGEN ML/L HIGH TIDE
OXYGEN ML/L LOW TIDE
BACTERIA PLATE COUNT THOUSANDS / ML HIGH TIDE
BACTERIA PLATE COUNT THOUSANDS / ML LOW TIDE
COLIFORM BACTERIA MPN / ML HIGH TIDE
COLIFORM BACTERIA MPN / ML LOW TIDE
MLW

FIG. 2. Distributions of properties in a longitudinal section of Raritan River at high and at low tides.

oxygen and salinity. The plankton tows were collected with a Clarke-Bumpus (1950) sampler using a No. 2-mesh net. The volume of water filtered during each tow was recorded.

Bacteriological samples were obtained with a modified ZoBell (1941) type water sampler at two or more depths at each station. A portion of each sample was plated for total bacterial counts on salt water nutrient agar (Reuszer 1933). These plates were counted after seven days. Coliform presumptive tests were made in triplicate in at least three dilutions, using lauryl sulfate Tryptose broth tubes ("Standard Methods," 1946). They were not confirmed or completed so that the discussion of coliform bacteria in this paper is not restricted to *Escherichia coli*. Oxygen concentration was measured by the Winkler method ("Standard Methods," 1946). The reagents for the oxygen analysis were added immediately after the collection of the sample. The titrations were done ashore. The bacteriological work was all done ashore, the samples being kept on ice until they could be treated, which was always accomplished within fifteen hours after collection.

Dr. Willem Rudolfs of Rutgers University kindly made available the facilities of his laboratory during our survey, and his cooperation is most gratefully acknowledged.

The distributions of properties observed at high and at low tide are shown in Figure 2. In these, and in subsequent figures, the distance scale is measured from the mouth of the river at Perth Amboy.

Near New Brunswick the salinity of the water was always low (less than 4 $^0/_{00}$). The source of the sea water in the area is a mixture of Hudson River water and sea water having a salinity of 27 $^0/_{00}$. The salinities observed at New Brunswick indicate that the water at this location contained between 85 and 96 per cent Raritan River water. The salinity gradually increased so that at Perth Amboy it was 21 to 24 $^0/_{00}$, giving concentrations of 22 to 11 per cent Raritan River water.

There was no measurable oxygen in the water at New Brunswick but the concen-

TABLE I. *Distribution of zooplankton in the Raritan River at high tide (numbers per liter of water)*

Miles from river mouth	Station	Cladocera	Protozoa and flagellates	*Acartia tonsa*	*Oithonina nana*
10.5	10 a	No living zooplankton			
	b	No living zooplankton			
9.5	9 a	No living zooplankton			
	b	No living zooplankton			
8.8	8 a	.18	.04		
	b	0	0	.07	
7.1	6 a	0	0	.58	
	b	0	0	2.50	
6.0	5 a	0	0	20.45	.80
	b	.33	0	44.6	1.67
6.0	5 b	.59	0	54.62	1.76
3.8	4 a	0	0	17.11	.76
	b	.21	0	33.24	3.43
0.25	1 a	0	0	31.44	.19
	b	.08	0	56.22	6.39

Note: a and b represent tows above and below the halocline.

TABLE II. *Distribution of zooplankton in the Raritan River at low tide (numbers per liter of water)*

Miles from river mouth	Station	Cladocera	Protozoa and flagellates	*Acartia tonsa*	*Oithonina nana*
10.5	10 b	0	.087	0	0
8.8	8 a	0	.016	0	0
	b	0	0	0	
7.1	6 a	0	0	0	0
	b	.033	0	0	0
6.75	a	0	0	.05	0
	b	.34	0	.34	0
6.0	5 a	0	0	.056	0
	b	.39	0	.69	0
6.0	5 a	0	0	0	0
	b	.03	0	.23	0
3.8	4 a	0	0	16.7	.91
	b	.98	0	111.71	7.67
0.25	1 a	0	0	0	0
	b	0	0	48.7	6.4

Note: a and b represent tows above and below the halocline.

tration of oxygen increased down river so that, at Perth Amboy, it was 65 to 75 per cent of the saturated value.

The total counts of bacteria remain nearly the same throughout the length of the river, though there was considerable variation in the numbers observed with depth. The coliform bacteria decreased from maximum values of 110,000 per ml. at New Brunswick to average values of less than 100 per ml. at the river mouth.

There were no living zooplankton in the water containing zero oxygen in the neighborhood of New Brunswick. Near the mouth of the river the zooplankton population was fairly high (more than 100 organisms per liter) and was made up of relatively few species, *Acartia tonsa* being predominant in all collections. The numbers of various species of zooplankton observed above and below the halocline at various locations are given in Tables I and II.

THEORETICAL CONSIDERATIONS

The primary objective of this investigation was to evaluate the effects of the various processes mentioned above in decreasing the population of coliform bacteria in the tidal reaches of the river. The technique which has been followed is based upon the concept that the population of coliform bacteria to be expected at any location within the tidal reaches of the river depends upon the original population in the undiluted river water which is progressively decreased by the bactericidal action of sea water, predation and dilution as the water traverses the estuary.

As the coliform bacteria are being transported downstream by the circulation of the water they are subjected to the bactericidal action of sea water. The number of coliform bacteria remaining in a given sample of water after taking account of this process is given by:

$$C_t = C_0 e^{-kt} \qquad (1)$$

in which C_0 and C_t are respectively the original count and the count after time t, and k is the coefficient of death rate.

The consumption of bacteria by zooplankton may be described in a similar way. Fuller (1937) has shown that the expected number of cells remaining in a given sample of water at the end of time t can be expressed by the equation:

$$C_t = C_0 e^{-wpt} \qquad (2)$$

in which w is the volume of water filtered per unit time, and p is the number of predators per unit volume.

These two equations may be combined to show the joint effects of mortality and predation as follows:

$$C_t = C_0 e^{-t(k+wp)} \qquad (3)$$

While the population of coliform bacteria is being decreased by the bactericidal action and by predation, the water is moving down the estuary and mixing with progressively greater amounts of sea water. It is necessary, for two

reasons, to define the circulation and exchanges of the water quantitatively. The rate of the circulation determines the length of time the population is exposed to the bactericidal action and to predation, and the dilution of the population is a direct consequence of the mixing of the fresh and salt waters.

An empirical theory which describes the circulation and exchanges of fresh and salt waters in tidal estuaries has been previously presented (Ketchum 1951). This theory permits the computation of the quantity of river water present in any part of the estuary and the length of time various proportions of the river water have been present within that part of the estuary. The application of the theory requires the subdivision of the estuary into volume segments defined horizontally by the width of the estuary and by the mean excursion of a particle of water on the flood tide. The quantity of water removed from such a segment on each tidal cycle is given by an exchange ratio derived from the volumes of water present at high and at low tides. The total quantity of river water accumulated Q_n in any segment n is a mixture of water of various tidal ages, so that:

$$Q_n = R[1 + (1 - r_n) + (1 - r_n)^2 + (1 - r_n)^3 + \cdots + (1 - r_n)^m] \quad (4)$$

in which r_n, the exchange ratio, is the ratio of the intertidal volume to the high-tide volume of the nth segment, R is the volume of water introduced by the river during a complete tidal cycle, and the superscripts 1, 2, $3 \cdots m$ refer to time in units of tidal cycles. As m approaches infinity this series approaches:

$$Q_n = \frac{R}{r_n} \quad (5)$$

If dilution were the only process active in decreasing the coliform population, the steady-state population, C_n, expected in the nth volume segment, could be obtained by multiplying the original concentration of bacteria in the undiluted source river water, C_0, by the average fraction of fresh water, F_n, in the segment, that is:

$$C_n = C_0 F_n \quad (6)$$

The average fraction of fresh water is given by the ratio between Q_n, the quantity of river water accumulated (equation 4), and the high-tide volume of the segment. It can also be computed from the salinity data of an hydrographic survey.

Before combining the biological and the circulation equations, however, the initial population of each segment must be expressed in terms of the concentration of bacteria entering that segment during each tidal cycle. This is necessary because, in traversing the estuary, the coliform population is reduced not only by dilution, as in equation (6), but also by the cumulative effects of the bactericidal action and predation in all of the intervening landward segments. The population entering the nth segment, $(C_0)_n$, is related to the population in the adjacent landward segment C_{n-1}, by the relationship:

$$(C_0)_n = C_{n-1} \frac{F_n}{F_{n-1}} \quad (7)$$

If dilution were the only process reducing the population, C_n would equal $(C_0)_n$ in each segment.

Each term within the brackets of the circulation equation (4) shows the proportion of water which has been within the segment for the period of time indicated by the superscripts. The biological processes have been reducing the bacterial population during the same period of time. The equations for the circulation (4) and for the biological processes (3) can be combined if time is expressed in units of tidal cycles, and if $(C_0)_n$ is substituted for the original population and C_n for the final population in equation (3).

$$Q_n C_n = R(C_0)_n[1 + (1 - r_n)e^{-(k+wp)} + (1-r_n)^2 e^{-2(k+wp)} + (1-r_n)^3 e^{-3(k+wp)} + \cdots + (1-r_n)^m e^{-m(k+wp)}] \quad (8)$$

This series approaches:

$$C_n = (C_0)_n \frac{R}{Q_n} \frac{1 - (1 - r_n)^m e^{-m(k+wp)}}{1 - (1 - r_n)e^{-(k+wp)}} \quad (9)$$

Since $(1 - r)^m$ and $e^{-m(k+wp)}$ both approach zero as the number of tidal cycles m approaches infinity, and since R/Q_n equals the exchange ratio, r_n, equation (9) may be reduced to:

$$C_n = (C_0)_n r_n \frac{1}{1 - (1 - r_n)e^{-(k+wp)}} \quad (10)$$

From this equation one can calculate the joint effects of dilution, bactericidal action and predation in decreasing the number of coliform bacteria down the length of the tidal estuary.

The relative importance of the various processes can be assessed by making the computations in sequence. For example, the effect of dilution alone can be computed by assuming k and wp to be zero, in which case $e^{-(k+wp)}$ becomes unity, the exchange ratio cancels out, and equations (7) and (10) are combined to give the dilution effect:

$$C_n = C_{n-1} \frac{F_n}{F_{n-1}} \quad (11)$$

The combined effects of dilution and bactericidal action can be calculated from equation (10) by assuming wp to be zero, when the bactericidal mortality becomes the only biological process considered. The time factor is inseparable from the circulation equation so that it is not possible to compute the biological effects alone.

The calculations described above are applicable to the high-tide distribution. The expected distribution at low tide can be most simply derived from the changes in location of the water as the tide ebbs. The estuary is segmented in such a way that the high-tide volume of each segment is equal to the low-tide volume of the adjacent seaward segment (Ketchum 1951). As a first approximation, therefore, the ebbing tide moves the water throughout the estuary one segment seaward. The populations at low tide are taken as equal to the population expected in the adjacent landward segment at high tide decreased by the predation and mortality due to bactericidal action which occur during a half tidal cycle. The empirical theory upon which these calculations are based assumes

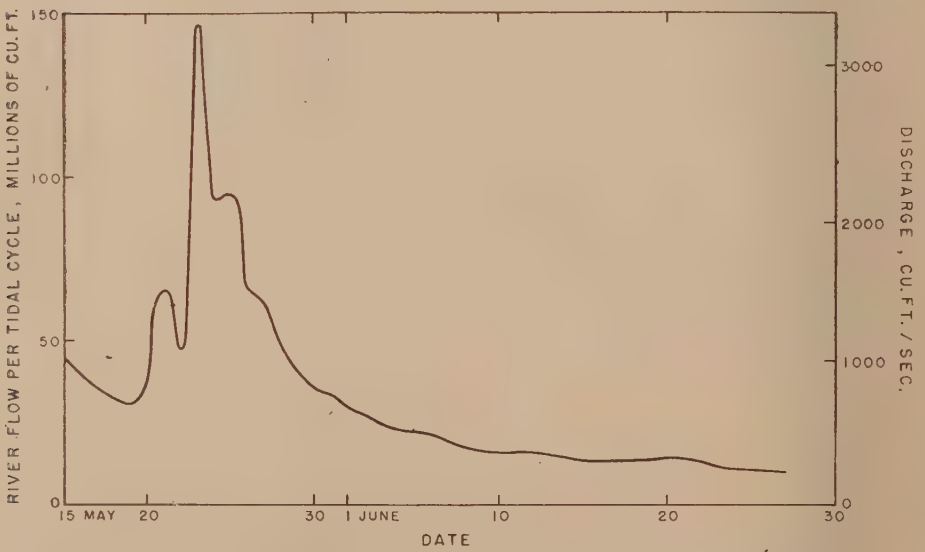

FIG. 3. River flow of the Raritan River during and prior to the time of the survey.

TABLE III. *The volumes of water, exchange ratios, and escaping volumes of river water for the various tidal excursion segments within the Raritan River*

Segment	Distance, miles*	Intertidal volume 10^6 ft.^{3}	High tide volume 10^6 ft.^{3}	River water volume 10^6 ft.^{3}	Exchange ratio r	Escaping volume fresh 10^6 ft.^{3}
1	11.77	16	20	18	0.80	14.5
2	10.10	30	50	42	0.60	25.2
3	8.10	39	89	60	0.44	26.4
4	6.20	46	135	66	0.34	22.4
5	4.53	65	200	74	0.325	24.1
6	2.75	130	330	86	0.39	33.6
7	0.9	220	550	98	0.40	39.2
8	0	274	774	113	0.354	40.0

* Distance from the river mouth to the center of the segment.

that the water in each volume segment is completely mixed at high tide. It will be recognized that this way of determining conditions at low tide does not take account of any additional dilution during the ebbing tide. As a first approximation this does not introduce any serious discrepancy in the results.

APPLICATION

Flushing of the estuary. Prior to the time of our survey the river flow was not constant, but decreased from a volume of 147 million cubic feet to a volume of 10.4 million cubic feet per tidal cycle. These river flow data are presented in Figure 3. Under such conditions a different volume of water will be moving through successive cross sections of the estuary. When the results of an hydrographic survey are available, however, one can compute the quantity of river water in each tidal-excursion segment (Tully 1949; Ketchum 1950). By applying the exchange ratio the volume of river water escaping through each cross section on the tidal cycle at the time of the survey can be estimated. This escaping volume of river water is, then, substituted for R in the equations. The necessary data for these calculations are given in Table III for the Raritan River at the time of our survey. The escaping volume of water was nearly constant throughout most of the length of the river, but it was lowest at the innermost segment, and highest at the mouth of the river. This variation would be expected from the change in river flow with time shown in Figure 3.

Bacterial population. In spite of the inherent variability of bacterial counting techniques, it is clear, from our data as shown in Figure 2, that the coliform population decreased from about 100,000 per ml. at the New Brunswick end of the river to less than 100 per ml. at the river mouth. The extremes of all of the counts obtained at high and at low tide at each station are plotted for the appropriate distance along the estuary in Figure 4.

The population of coliform bacteria expected at various locations as the result of dilution, dilution and mortality, and dilution, mortality and predation, are shown in Table IV, and are also plotted for comparison in Figure 4.

All of these calculations of expected populations depend upon the selection of the initial population size, which should be the population in the undiluted river water at New Brunswick. Five separate water samples at this location contained 96 per cent river water on the average, and gave counts of 110,000 cells per ml. It has been concluded from these observations that the population in the undiluted river water at the time of our survey was 115,000 cells per ml. At Perth Amboy the average population was 30 cells per ml. at high tide and 130 cells per ml. at low tide.

Dilution. The effect of dilution can be directly determined from the proportion of fresh water in each sample. On the

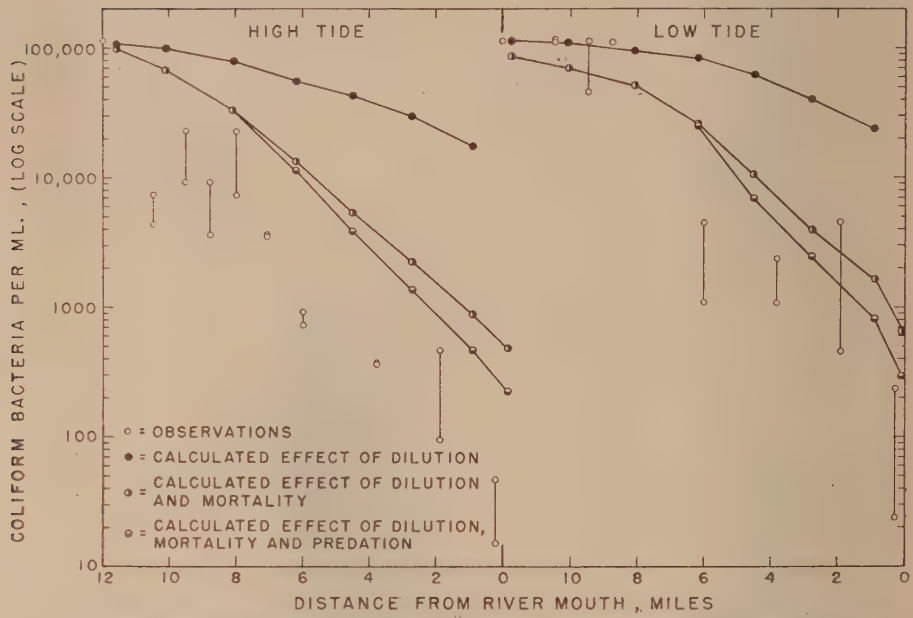
HIGH TIDE
LOW TIDE
COLIFORM BACTERIA PER ML., (LOG SCALE)
100,000
10,000
1000
100
10
○ = OBSERVATIONS
● = CALCULATED EFFECT OF DILUTION
◑ = CALCULATED EFFECT OF DILUTION AND MORTALITY
◒ = CALCULATED EFFECT OF DILUTION, MORTALITY AND PREDATION
12 10 8 6 4 2 0 10 8 6 4 2 0
DISTANCE FROM RIVER MOUTH, MILES

FIG. 4. The observed population of coliform bacteria in the Raritan River, and the populations expected as a result of dilution, of dilution and mortality, and of dilution, mortality and predation.

average, the water at New Brunswick (segment 2, 10.1 miles) was 85 per cent fresh at high tide, and 96 per cent fresh at low tide. At the mouth of the river the proportions were 14.5 per cent at high tide and 15 per cent at low tide. Through the course of the river, if dilution were the only process affecting the bacterial

TABLE IV. *Numbers of coliform bacteria expected in the various tidal excursion segments of the Raritan River*

Population expected (cells/ml.) as a result of:

Tide condition	Segment number	Average fraction fresh	Dilution	Dilution and mortality*	Dilution mortality* and predation
High	1	0.90	104,000	93,200	93,200
	2	0.85	98,000	68,000	68,000
	3	0.68	78,000	34,800	34,600
	4	0.49	56,400	13,600	11,200
	5	0.37	42,500	5,360	3,830
	6	0.26	30,000	2,230	1,360
	7	0.15	17,200	885	475
	8	0.145	16,700	472	214
Low	1	1.00	115,000	86,000	86,000
	2	0.96	110,000	70,000	70,000
	3	0.85	98,000	51,000	51,000
	4	0.73	84,000	26,100	26,000
	5	0.55	63,250	10,200	8,400
	6	0.35	40,200	4,000	2,900
	7	0.21	24,200	1,700	1,200
	8	0.15	17,200	655	350

* In this table and in Figure 4, mortality refers specifically to the computed effects of the bactericidal action of sea water.

numbers, the population should decrease proportionately, *i.e.,* to 16,700 at high tide and to 17,200 at low tide. It is obvious that dilution accounts for only a small part of the observed decrease, since these numbers are more than 100 times as great as the observed final populations.

Dilution and mortality. Two samples of surface water, collected at Stations 1 and 5, were analyzed for bactericidal activity by the methods previously described by Vaccaro *et al.* (1950). In both of these experiments the coefficient of death rate [2] was 1.15 days^{-1}, or 0.578 tides^{-1}. This coefficient has been used in calculating the effect of the bactericidal action of sea water.

The combined effects of dilution and the mortality due to the bactericidal action are sufficient to reduce the coliform population, as the water moves down the Raritan River, from an initial value of 115,000 per ml. to 472 per ml. at high tide, and to 655 per ml. at low tide. These two processes combined account for much of the decrease, since these numbers are only five to fifteen times as great as the observed final populations.

Dilution, mortality, and predation. It is also possible to make an approximate estimate of the importance of predation from the available data and published information. It should be emphasized, however, that this is undertaken merely to assess the relative importance of this process, and the results herein quoted are only first approximations. Fuller (1937) has studied the consumption of a small diatom *Nitzschia Closterium* by *Calanus finmarchicus* and found that the animals removed all of the diatoms in 0.2 ml. of water per hour. With two species of larger diatoms, the cells present in 3 to 8 ml. of water were consumed per hour (Harvey 1937). Thus it appears that calanoid zooplankton could be expected to filter living organisms from 12 to 192 ml. of water per day. With forms as small as the coliform bacteria it might be reasoned that the effective filtration would be closer to the lower value, though it is not actually known whether the zooplankton are able to remove bacteria from the water.

It should also be recognized that the species of zooplankton found in the Raritan River are not the same as those used in the above-quoted experiments.

In spite of these limitations it would appear to be advantageous to evaluate the possible effect of predation in determining the distribution of coliform bacteria. This has been done, making the assumption that the zooplankton organisms observed in the Raritan River might be expected to remove the bacteria contained in 20 ml. of water each day (10 ml. per tidal cycle).

The results of these calculations are also shown in Table IV and in Figure 4. In the upper end of the river there is no effective predation since no living zooplankton were collected in the tows obtained at these locations. By the time the circulation has brought the water to the mouth of the river the predation effect, as calculated, would decrease the bacterial population to about one-half of the population which would survive as a result of dilution and bactericidal action. This would give populations of 214 and 350 at high and low tides. These numbers are only 3 to 7 times as great as the observed final populations.

The observed decrease in the size of the population was from an initial concentration of 115,000 cells per ml. to final concentrations of 30 cells per ml. at high tide and 130 cells per ml. at low tide. The observed decreases are, therefore, 114,970 and 114,870 for high and low tides. The decreases which are expected as a result of the joint action of dilution, bactericidal action and predation are 114,786 and 114,650 at high and at low tides. These calculations thus account for more than 99 per cent of the observed decrease. The

[2] In our previous work the coefficient of death rate has been calculated for base 10 logarithms. For the present purpose the coefficient is expressed in terms of base *e* logarithms, *i.e.,* 2.303 times the value of the coefficient as previously defined.

decreases are so large, however, that in spite of this agreement, the calculated populations at the mouth of the river are several times greater than the average observed populations.

Discussion of Results

Rudolfs and Fletcher (1951) made an extensive survey of the pollution of Raritan River and Bay in 1950. Their average results indicate that the worst condition for the river was found just below New Brunswick, where the oxygen content approached zero and the mean coliform count was 62,000 per ml. At Victory Bridge (our station 2, Fig. 1) the dissolved oxygen saturation was increased to an average of 51.5 per cent and the mean coliform counts decreased to 440 per ml. Our observations are in substantial agreement with the results of Rudolfs' and Fletcher's extensive survey. They comment on the considerable change which has occurred in the river since the survey made by Rudolfs and Heukelekian (1942).

The calculations presented indicate that the joint effects of dilution, bactericidal action of sea water and predation by zooplankton are sufficient to account for practically all of the disappearance of coliform bacteria throughout a ten-mile length of the Raritan River. The effects of the three processes are cumulative factorially, and the relative effectiveness of each process can be conveniently expressed by the ratio of the computed populations in each segment (Table V). The effect of dilution, which acts on all materials in the water equally, is assigned a relative effectiveness of unity. When the population expected as a result of dilution is divided by that expected as the cumulative result of dilution and bactericidal action, the relative effectiveness of the latter process is obtained. When the population expected as a result of both dilution and bactericidal action is, in turn, divided by that expected as a result of predation in addition to these two processes, the relative effectiveness of predation is obtained.

In the river end of the estuary the effect of the bactericidal process is not very much greater than that of dilution. As the water moves down the estuary the increasing time greatly increases the effectiveness of the bactericidal action until, at the mouth of the river at high tide, this process has accounted for thirty-five times as much disappearance as has dilution. At low tide, when the water at the mouth of the estuary has not been within the estuary for so long a period of time, the effect of this mortality is twenty-six times as great as that of dilution. Similarly, the effect of predation increases as one moves down the estuary until it is ultimately twice as great as the dilution effect. The residual disappearance of bacteria which is not accounted for by the three processes considered would, at the river mouth, indicate that the unevaluated processes are more important than dilution or predation, but much less important than the bactericidal action of sea water. The observed average population of 30 and 130 cells per ml. at high and low tides, would indicate that the relative effectiveness of unevaluated processes was 7 to 3 times as important as dilution.

It is of interest to speculate concerning the unevaluated disappearance of coliform bacteria. Sedimentation and the resultant accumulation of the bacteria on the bottom

Table V. *The relative effectiveness of dilution, bactericidal action, and predation in decreasing the coliform bacteria in the Raritan River*

Tide condition	Segment	Dilution	Bactericidal action	Predation
High	1	1.00	1.12	1.00
	2	1.00	1.44	1.00
	3	1.00	2.24	1.00
	4	1.00	4.15	1.21
	5	1.00	7.94	1.40
	6	1.00	13.4	1.64
	7	1.00	19.4	1.86
	8	1.00	35.4	2.20
Low	1	1.00	1.34	1.00
	2	1.00	1.57	1.00
	3	1.00	1.92	1.00
	4	1.00	3.21	1.00
	5	1.00	6.20	1.21
	6	1.00	10.0	1.38
	7	1.00	14.2	1.67
	8	1.00	26.3	1.82

could be expected to have a significant effect on the population in the water. Weiss (1951) has shown that when silts are centrifuged from river waters as much as 50 per cent of an *E. coli* population may also be removed. When mixtures of sea water and river water were used the removal of *E. coli* was less effective. Our survey did not provide the data necessary to evaluate the effect of sedimentation, but it seems probable that this process could account for much or all of the residual disappearance of bacteria within the river.

It is also possible that the coefficients of mortality and of predation used in these calculations are lower than those actually obtaining in the river at the time of our survey. Vaccaro *et al.* (1950) observed coefficients of mortality as great as 2.88 days^{-1}, a value more than twice as great as the one observed on Raritan River water. The population expected at high tide at the mouth of the river using this coefficient of mortality would be 91, or less than one-fifth of the population predicted in Table IV. If one were to assume that the predation effect was the maximum observed, namely that the zooplankton would filter 100 ml. of water per tidal cycle instead of 10, as used above, a further decrease to 36 cells per ml. would be expected. This concentration is virtually identical with the average value of 30 cells per ml. observed at this location at high tide. The coefficients used in the calculations were selected as the most probable values, but it is clear that coefficients within the possible limits could be chosen so that the calculations would fit the observations more precisely.

Summary

1. The distributions of salinity, oxygen and bacteria in the Raritan River are described.

2. A method is presented for evaluating the relative effects of dilution, the bactericidal action of sea water and of predation in reducing the population of coliform bacteria in a tidal estuary.

3. It is shown that these three processes account for more than 99 per cent of the decrease in coliform bacteria in the Raritan River. The bactericidal action is the most important process, followed by predation and dilution.

4. Unevaluated processes contributing to the decrease are more important than dilution or predation but much less important than the bactericidal action.

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INITIATION OF CAMBIAL ACTIVITY IN SOME FOREST TREES IN ONTARIO [1]

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INTRODUCTION

The modern concept of secondary growth seems to have had its birth some 250 years ago. In 1708 de la Hire, in a work reviewed some 145 years later by Thomas Hartig (1853), quoted another investigator to the effect that in buds and roots, in the space extending downward between the wood and bast, there is a tissue which through its equal-sided division gives rise to new wood and bast units. Hartig himself was in agreement with this and did much to establish its validity as opposed to such other contemporary theories as that of transformation of bast into wood or the theory which considered the cambium as a nutritive fluid comparable to blood in the animal body.

In the temperate regions, there is a considerable portion of each year in which the cambium is inactive and a number of investigators have concerned themselves with its resumption of activity in the spring. Thomas Hartig (1853) concluded that, in general, radial growth began at the tips of twigs and then gradually extended downward. He noted some exceptions however, mentioning a 30 year-old Scotch pine and an oak where cambial activity began almost simultaneously over the entire trunk. According to Mer (1892), cambial activity in oak, beech, basswood, fir and other trees of 25 years of age and under, begins in the youngest twigs. In older trees he described it as simultaneous at the bases of branches and along the trunk. Robert Hartig (1892) found that in isolated trees cambial activity started in all parts of the trunk at approximately the same time, whereas under forest conditions its initiation occurred first in the twigs whence it proceeded downward, the cessation following the same order. Hastings (1900) stated that in broad-leaved trees, radial growth did not begin until the buds opened. This has been corroborated by Buckhout (1907) and Priestley (1930).

Brown (1912, 1915) working on pitch pine (*Pinus rigida* Mill.) and white pine (*Pinus strobus* L.) came to the conclusion that cambial activity was initiated some distance below the apex and developed in both directions. He considered that growth in the side branches followed the same course. Knudson (1913) working on larch (*Larix laricina* (Du Roi) Koch.) was in agreement with Brown. It may be noted that in both these investigations the amount of material was not large. Knudson in his paper suggested the desirability of further investigation. The pertinence of this suggestion is confirmed by Priestley's work (1930) which has led him to differ with Brown and Knudson and agree with Thomas Hartig, that the initiation of cambial activity occurs at the base of opening buds. Wareing (1951) noted that rapid initiation of cambial activity throughout the tree is characteristic of ring-porous species as a class. Diffuse-porous species, on the other hand, are much slower in the basipetal movement of cambial activity in the spring. He stated that the failure to make distinction between the behavior of the two types of species may partly account for the conflicting results obtained by earlier workers.

Concerning the cause underlying the initiation of cambial activity in spring, two theories formed the basis of a controversy between R. Hartig (1892) and L. Jost

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(1891) 60 years ago and since that time no new theories have been evolved. Hartig's contention was that the stimulus to the cambium came from the bud and developing leaves in the form of increased food supply whereas Jost believed the initiation of growth was connected with a stimulus proceeding from the same source but not connected with the food supply. Later, after the discovery of auxins, Jost (1941) identified this material as the stimulus which he had postulated, and proved experimentally that it did stimulate the cambium to activity. Other workers also came to the same conclusion (Snow 1935; Brown and Cormack 1937).

Methods for Recording Radial Growth

Various methods have been employed in the study of cambial activity in forest trees. Jost (1891) and Hartig (1892) studied periodic growth by selecting even-aged stands where samples could be obtained from trees felled at different times during the growth period. Results obtained by this method were complicated by inter-tree variability. Von Mohl (1862) and others used calipers and tapes to measure the tree bole and this method is still widely used where great accuracy is not essential. MacDougal (1938) developed a very efficient dendrograph which has been used by a number of workers. The apparatus is so planned that without significantly affecting the cambium, two areas of contact are maintained on opposite sides of the trunk and even very small changes in diameter are recorded on a revolving drum by means of a set of levers connected with these contacts. The apparatus is, however, rather expensive and a separate instrument is required for each tree under observation.

In recent years, instruments known as dendrometers have been developed which allow the course of radial increment throughout the year to be followed in many trees with a single instrument. All of these operate on the principle of measuring the change of distance between a plate fastened to the bark, and a reference plane anchored in the wood. Successive dendrometer measurements permit the calculation of radial increase with time.

Several dendrometers have been described (Reineke 1932; Daubenmire 1945; Warrack and Jorgensen 1950) employing dial gauges with various means of application to the tree. During current studies a dendrometer was developed (Belyea, Fraser, and Rose 1951) which has advantages over earlier types. A standard dial gauge graduated in thousandths of an inch is mounted on a triangular base. Through an aperture in the center of the base projects a moveable spindle. The spindle is connected with the apparatus so that as it moves up one-thousandth of an inch, the needle on the dial moves over a distance of one unit. From the angles of the base, three pointed legs project downward. When the instrument is in use, the three legs are applied to the heads of three screws which are permanently inserted deep into the wood of the tree, while the moveable spindle impinges on the flat head of a thumb tack glued to the bark. In this manner any radial increment is registered in the dial gauge by differences in readings.

A dendrometer merely records total radial increment. In the present investigation it was important to distinguish increment by swelling from that caused by cell division. For this reason methods based on sampling and microscopic study were also used. In the early stages of the work, the samples were removed with a hammer and chisel, but later another method was devised which produced less injury to the tissues. In this later procedure use was made of a steel cutting tube which consisted of a three-quarter-inch hardened steel pipe ground to a sharp chisel edge at one end. After the outer part of the dead periderm had been carefully chipped away, the cutting tube was driven in to delimit the segment. A chisel was then inserted beside the cutting tube and served as a lever to ensure that the delimited segment was removed from the

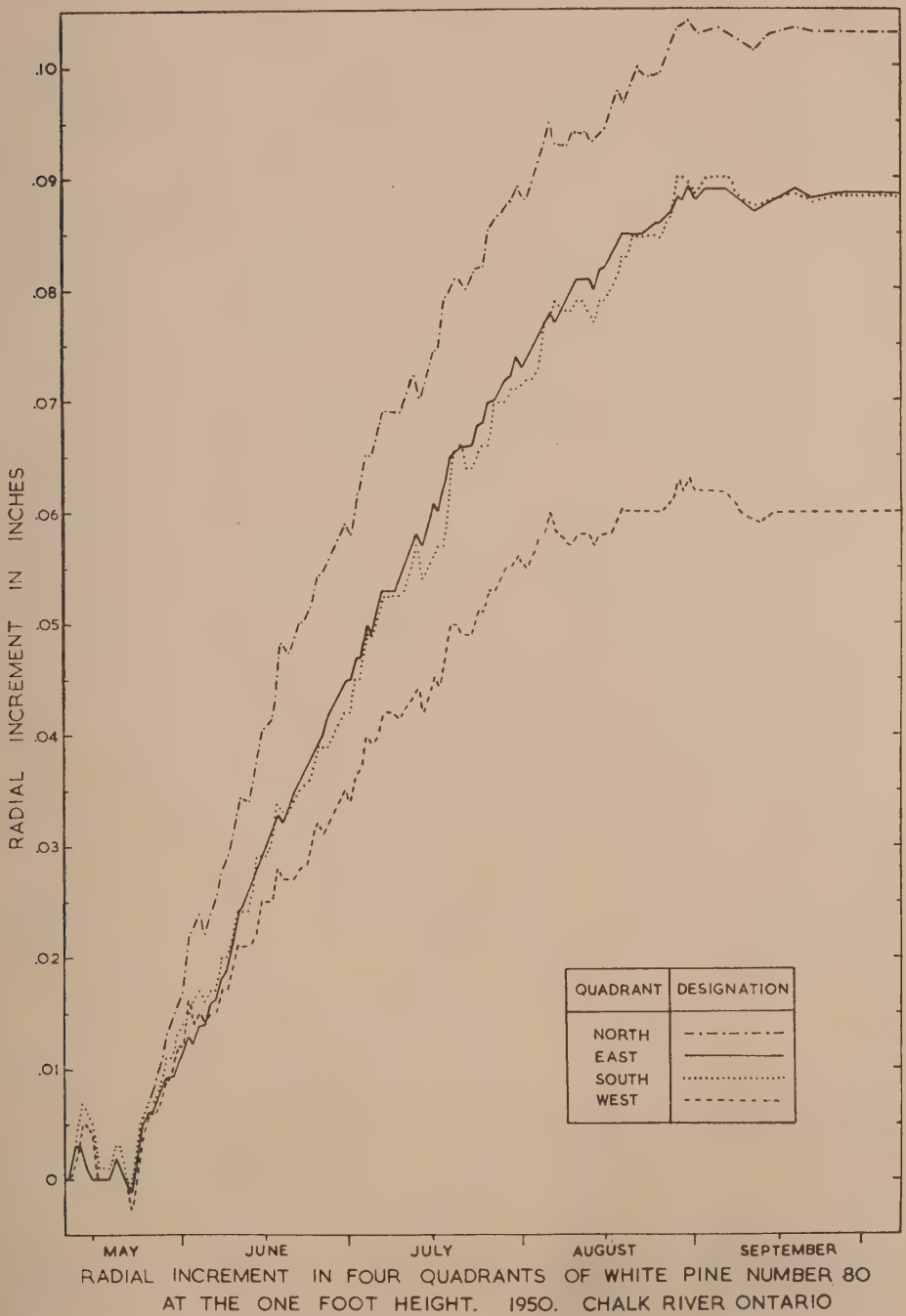

FIG. 1. Seasonal march of radial increment, as measured with a dendrometer, on four sides of a white pine.

tree with the tube. The segment was pressed out of the tube by means of a wooden rod. It was then trimmed, labelled as to date, height, and tree, and preserved in 70% alcohol. This process produced less injury to the delicate tissue than was produced in earlier operations with the chisel alone.

Neither dendrometer nor sectioning can give a completely accurate picture. The former, as mentioned above, merely records total radial increment without distinguishing changes caused by cell division and swelling whereas the latter method is open to criticism for a number of reasons. Each sample taken leaves a wound which may affect subsequent growth and successive samples cannot be taken from the same position with the result that the variation in the amount of cambial growth on different sides of the tree complicates the results. Such variation is especially evident in the large side branches, but is by no means confined to this region. Figure 1 illustrates the kind of variation which may be expected on an apparently smooth and evenly developed trunk. The four curves record daily measurements of radial increment taken at permanently fixed points, one foot from the ground on four sides of the trunk of a white pine (*Pinus strobus* L.) (No. 80 in the present investigation). All the readings were made between 8 and 9 A.M. to minimize error caused by diurnal fluctuations of temperature and moisture. These variations in radial increment were noted by an experiment. In addition to the morning measurements, readings were taken in the evening between 8 and 9 P.M. The records (Table I) indicate that in almost every case there was loss of increment during the day, presumably caused by dehydration of tissues. MacDougal (1938) and more recently Byram and Doolittle (1951) have also noted such changes.

There was no difference in time of initiation of radial growth in the four quadrants of the tree. In all quadrants the initial measurements indicated a series of fluctuations from May 11 to May 23, all four curves following practically the same path. Similar fluctuations occurred in all trees studied and seemed to be the result of hydration of the tissues as the rise of sap began. During this period the tissues contained sap under pressure as evinced by bleeding where a wound had been made. By the latter date the trunk had returned to its size noted on May 10, and at that time permanent increment began, presumably connected with cell division, and continued throughout the period of cambial activity. Soon after this, variation in rates of radial increment became observable by a spreading on the part of the curves. Experience has shown that while the small irregularities in the curves are due to moisture and temperature changes, their general trend is associated directly with cambial activity, and a difference of 0.04 inches (the thickness of some 20 to 30 tracheids) between the ends of the curves for the north and west sides, respectively, indicates variation of cambial growth for the season. On the other hand the curves for the east and south sides are practically parallel except for slightly greater fluctuations on the south side.

Although for the current year's growth, the exact number of rows of tracheids may be distinguished, the case is different for

TABLE I. *Changes in radial increment during day (0800–2000) and night (2000–0800) periods June 1, 2, 3, 1950, White pine no. 80*

Date	Time	Root	1′ North	1′ East	1′ South	1′ West	15′
June 1	0800–2000	−.001*	−.002	−.003	−.003	−.004	−.004
1–2	2000–0800	+.001	+.002	+.003	+.002	+.002	+.004
June 2	0800–2000	000	−.002	−.003	−.001	−.003	−.005
2–3	2000–0800	000	+.004	+.004	+.003	+.004	+.004

* Measurement in thousandths of an inch.

TABLE II. *White pine no. 82—trunk—Plot A 2—Chalk River—1950*

Height:....	1′			10′			24′		
Date	No. Type*	Width (micra)	Dendr. (micra)	No. Type	Width (micra)	Dendr. (micra)	No. Type	Width (micra)	Dendr. (micra)
May 20	Swelling, no tracheid differentiation		175	5 SpTr	120	255	7 SpTr	130	250
30	4 SpTr	85	575	8 SpTr	250	750	11 SpTr	380	730
June 15	16 SpTr	560	1200	15 SpTr 11 SiC	510 120	1250			
23	20 SpTr	850	1400	28 SpTr	1200	1400	33 SpTr	1290	1600
30	27 SpTr	1200	1600	43 SpTr	1360	1700	40 SpTr	1360	1950
July 8	43 SpTr	1700	1850	36 SpTr 12 CC	1350 250	1900	27 SpTr	1350	2200
15	30 SpTr	1400	1950	60 SpTr 12 CC	2100 250	2050	64 SpTr 10 CC	2400 180	2600
29	35 SpTr	1450	2300	68 SpTr	3100	2500	80 SpTr 22 SiC	2300 510	3250
Aug. 5	34 SpTr 12 SiC	1400 340	2500	45 SpTr 12 SiC	2100 260	2600	70 SpTr	2600	3500
13	76 SpTr 14 SiC	3000 340	2500	50 SpTr	2100	2600	55 SpTr 18 SiC	2200 420	3600
20	35 SpTr 16 SiC	1300 210	2800	35 SpTr 6 Sic	1450 170	2700	48 SpTr	2000	3800
26	82 SpTr	3800	2900	69 SpTr 12 SiC	3000 340	2800	60 SpTr 10 SuTr	2600 340	3900
Sept. 5	74 SpTr	3400	3000	40 SpTr 9 SuTr 6 CC 22 SiC	1500 80 24 250	2900	52 SpTr 16 SuTr 20 SiC	2400 250 210	4000

* SpTr—Spring Tracheid
SuTr—Summer Tracheid
CC—Cambial Cell
SiC—Sieve Cell

phloem where there is a gradual transition from mature, undistorted tissue to cells crushed by radial pressure, and the delimitation of the current year's growth is unreliable. Thus, measurements obtained from sections, to be accurate, must only apply to wood and will be smaller than those obtained by the dendrometer.

Another drawback of the sampling method of study lies in the fact that delicate tissues in the cambial region are sometimes destroyed in the sampling and the extent of such destruction will be discovered only when the sections are prepared and it is too late to get another sample.

The results recorded in Table II indicate the extent of this difficulty and provide, as well, a comparison between the data obtained by the two methods. The table records an experiment made for this purpose on a trunk of a white pine (No.

82 at Chalk River, Ontario). Samples were taken on the dates recorded in the left hand column of the table at heights of 1, 10 and 24 feet respectively. These samples were all sectioned and the cell layers produced by the cambium were counted and measured in so far as this was possible, the results being recorded in the first three columns under each height in the table. The first column indicates the number of layers, the second the kind of element composing them, whether spring tracheid, summer tracheid, sieve tube or cells where no differentiation was observable beyond vacuolation, and the third column gives measurements in micra. The fourth column under each height records dendrometer measurements (converted to micra) made at the same time the samples were taken.

The limitations of each method are observable in the table. It will be noted for example, during the month of June, when growth was most rapid no undifferentiated cells are listed at any height in the tree. This is due to the fact that although the greatest care was exercised, and the cutting tube produced less damage than when the chisel was used, the extremely fragile cells of this region were destroyed. As a matter of fact the number of undifferentiated cells recorded in the whole table is very small. The numbers of sieve tubes also are irregular and one cannot be sure to what extent this is due to crushing of younger cells when sampling, or older cells crushed during the course of growth, or differences in cambial activity on different sides of the tree. The variations in number of fully formed tracheids, for example, those noted at the 1-foot height on July 8 and 15, are undoubtedly due to the last named cause. The sampling method on the other hand does provide a means of ascertaining in what part of the tree the seasonal production of secondary growth was initiated. For once a new tracheid has been formed it can be seen and recognized. Dendrometer readings are less reliable in this respect because of initial swelling which has been pointed out and is again evident in this table. They show a rather regular increase in girth throughout the season. It is notable that for the period from August 5–13 the dendrometer shows no increment at the 1 and 10 foot heights and a comparatively small one at the 24 foot level. This was a week when no rain was recorded in the area and soil moisture units under the tree indicated the most pronounced drought of the season. The limitation of both methods is well indicated here, for from neither can information be obtained as to whether this cessation of growth was caused by drying out of tissue, the lessening of cambial activity, or both.

Initiation of Cambial Activity

Since the work of Brown and Knudson on the initialtion of cambial activity, the tendency has been to accept their conclusions as applicable to trees growing in our climate. For example, Eames and McDaniels (1947) state: "There is no uniformity in the position of first growth in the cambium; this is often in the central part of the tree, extending then to all parts, but cambial growth may also start at the base of the tree or at tips of twigs." While Priestley's results (1930) were in agreement with those of earlier European workers suggesting the initiation of cambial activity at tops of trees and tips of branches, he went on to say, "we must remember, in connection with the North American work, that what is seen in spring may be the resumption of cambial activity at a point where it was arbitrarily stopped in the autumn by the advent of freezing temperatures, and that conditions may be different where the winter is milder." In view of this and the importance of the problem from the standpoint of deciding the nature of the stimulus to renewed cambial activity, it seemed worthwhile to make some observations on Canadian trees. For this phase of the investigation, three individuals of white pine growing on different sites were chosen. This was one of the species used by Brown (1915) in his work. The re-

sults obtained were checked with three other species, namely tamarack (*Larix laricina* (Du Roi) K. Koch), black spruce (*Picea mariana* (Mill.) BSP) and white birch (*Betula papyrifera* Marsh.) and by a series of dendrometer measurements on three other white pines.

The first pine to be reported on was a 90-year-old tree, 55 feet high, with a trunk diameter of 16 inches at four feet from the ground. It was growing in a deep bog, 16 miles north of Toronto, surrounded by small trees of tamarack and black spruce with an undergrowth of pale laurel (*Kalmia polifolia* Wang.) labrador tea (*Ledum groenlandicum* Oeder.), leather-leaf, (*Chamaedaphne calyculata* (L.) Moench.) and *Sphagnum* sp. The water table was frequently on the surface until the end of June. The lowest limbs were 15 feet from the ground and unshaded by the surrounding trees.

Samples were taken with a hammer and chisel at heights of 1, 20, 30 and 40 feet above the ground. The four sections of the first set were taken as far as possible in a vertical line up the south side of the trunk, and those of the succeeding sets were separated by a lateral distance of approximately one inch. No cambial activity was discernible when the first samples were taken on April 28, 1948. Those secured on May 17 showed no sign of cell division in the cambium at any of the four heights. Swelling in the cells of the cambial region was observable at the one-foot and 20-foot heights, but not above this. This swelling of the cambium at the lower levels appeared to mark the upward passage of sap. The sampling data for May 27 and June 10 are outlined below.

The second white pine was 35 years old, 35 feet high, with a trunk diameter of eight inches at the four-foot level. It was 50 yards northeast of the tree just described, and about 30 yards from the edge of the bog. It was not crowded by other trees and had branches to within six inches of the ground. It was sampled at heights of 1, 15 and 30 feet. Samples obtained from all heights on April 28 and May 17 indicated no cambial activity.

The sampling data for May 27 showed three layers of tracheids with thickened, partly lignified walls at the 30 foot height. The walls of the three layers of tracheids formed at the 15 foot levels were only thickened in the vicinity of the radial pits and had, as yet, no lignification. At the 1 foot level no new tracheids had differentiated. By June 10, new tracheids were being formed throughout the trunk.

White pine No. 3 was 55 years old, 60 feet high, with a trunk diameter of 15 inches at the four-foot level. It was on a dry sandy ridge, one-half mile south of the previously mentioned bog, and was surrounded by a mixed growth of yellow birch (*Betula lutea* Michx. f.), aspen (*Populus tremuloides* Michx.), red oak (*Quercus rubra* L. var. *borealis* (Michx. f.) Farw.), beech (*Fagus grandifolia*

Observations May 27

Cutting height		Total width (micra)
40′	Four layers, differentiating tracheids, wall thickened but no lignification.	98
30′	Three layers, differentiating tracheids, wall thickening, but no lignification.	53
20′	Two layers, undifferentiated tracheids, no thickened wall discernible.	30
1′	One layer, undifferentiated tracheid, swelling but no thickened wall or lignification.	24

Observations June 10

40′	Four layers, spring tracheids, with thickened lignified wall.	136
	Four layers, differentiating spring tracheids, with unthickened wall.	120
	Cambial zone of 10 undifferentiated cells.	97
30′	Two layers, spring tracheids with thickened lignified wall.	71
	Two layers, differentiating tracheids with unthickened wall.	55
	Cambial zone of 7 undifferentiated cells.	84
20′	Two layers, spring tracheids, with partly thickened wall, slightly lignified.	90
	Cambial zone of 9 undifferentiated cells.	84
1′	One layer, differentiating tracheid, no thickened wall or lignification.	34

Ehrh.), and hemlock (*Tsuga canadensis* (L.) Carr.). The lower branches (between 15 and 25 feet from the ground) were all dead presumably because of shade from the adjacent trees.

There was no cell division in samples taken April 28 at the 50, 40, 30, 15 and 1 foot levels. The cambial zone consisted of eight layers of undifferentiated cells. Its total width at the upper levels was 70 micra but it was slightly swollen to a thickness of 77 micra at the one-foot height. By May 17 three layers of tracheids were forming at the 50′ and 40′ heights, two layers at 30′ with no cambial activity at the lower levels. By June 10 the cambium was active throughout the trunk.

The results obtained from these three trees consistently indicate that the march of initiation of cambial activity is from above downward. In common with the work of a number of previous investigators, the results have one weakness in that the observations did not extend to the extreme tip of the tree where it was impossible to take a series of successive samples. In so far as they go, the results are in agreement with Priestley and earlier European workers.

In the bog already referred to, there was an even-aged stand of tamarack and black spruce. These were used for a series of observations following the method of von Mohl who used a separate tree for each sample series. The disadvantage of this method is evident. The advantage is that it enables the sampling to be carried right to the tip of the tree, there being no objection to the destruction of the leader. A special effort was made to choose trees of the same size (ten feet) and the branching extended to the ground in all cases. Observations on these trees were as follows:

TAMARACK

Observations May 27, 1948

Cutting height		Total width (micra)
10′	2 layers, spring tracheids, thickened lignified wall.	34
1′	No cell division discernible.	

Observations June 10

10′	6 layers, spring tracheids, thickened lignified wall.	84
1′	2 layers, spring tracheids, thickened lignified wall.	63

BLACK SPRUCE

Observations May 27

Cutting height		Total width (micra)
10′	2 layers, spring tracheids, thickened lignified wall.	42
	1 layer, differentiating tracheid, thickening wall, unlignified.	20
1′	Cambial zone swelling but no differentiating tracheids.	

In both the tamarack and black spruce, no cambial activity was observed prior to May 27, and by June 10 the cambium was active at all levels. The observations on these two species are in agreement with those of the larger white pine trees, and supplement the former evidence in that observations were carried to the extreme tip of the tree. In both species cambial activity began at the tip of the tree between May 17 and May 27 at which time there was no sign of growth at the base. Moreover, in additional trees sampled up to July 13, the upper part was always in advance of the lower.

Little work of this kind was done on deciduous trees but an experiment was planned with an individual white birch. In some respects this experiment was unsuccessful due to the unexpectedly rapid initiation of radial growth throughout the tree but it did provide one point of interest.

The white birch was 40 years old, 35

feet high with a trunk diameter of 14 inches at the four foot level. It was on a well drained sandy loam in a small clump of birch and aspen in the Don River valley, near Toronto. Samples were obtained at the 30, 15 and 1 foot levels. Those taken April 30, May 3, May 9, and May 19 showed no indications of division in the cambium although swelling was observed in the lower parts of the tree as early as April 30. By June 3 when the next samples were taken, cambial activity had begun at all levels. However, on May 19 several twigs were collected from tips of branches and all showed cambial growth near their tips with a layer of this season's wood up to 90 micra, composed usually of one vessel and a number of fibers. Thus, although the course of initiation of cambial activity throughout the tree was not established, it did become evident that its first initiation was near the tips of twigs.

The fourth white pine studied (No. 82 at Chalk River) was 25 years old, 30 feet high, with a trunk diameter of seven inches at the four-foot level. It was on a dry, loamy sandy till on the Petawawa Forest Experiment Station, Chalk River, Ontario, and was surrounded by a mixed growth of red oak, white birch, and white spruce (*Picea glauca* (Moench) Voss). This tree had been repeatedly attacked by the white pine weevil (*Pissodes strobi* (Peck)) with the consequent destruction of the leader. This had occurred at the ten foot level where the lateral branches developed very strongly and one of them had assumed the vertical position of the leader. Destruction of the main shoot above the 25-foot height resulted in the production of dual trunks of equal form, from former lateral branches. The branching extended to within five feet of the ground.

Dendrometer reference sites were established at the 24, 20, 15, 10, 5 and 1 foot heights as well as on the upper side of a root 18 inches from the trunk base. Daily measurements at all levels are recorded for the May 15–June 15 period in Figure 2. Results from sampling at 24, 10 and 1 foot levels have already been referred to in Table II.

Swelling and probably cambial cell division had already taken place before the first records were made but for the first few days of the observations there was no differentiation of tracheids at the one-foot level. In each curve there is at first a rather steep rise followed by a flattening off which lasts for some days. After the end of this flat region, there is a consistent rise continuing throughout the rest of the curve unless some very drastic modifying factor is brought to bear. In the present tree, the horizontal section of the curve lasts from May 16 to May 21. The latter date is apparently the time when increment by cambial divisions become important as opposed to the more fluctuating type caused by hydration and swelling of tissues. From Table II it will be seen that by May 20 seven layers of spring tracheids with a thickness of 130 micra had been formed at the 24-foot level, and five spring tracheids of 120 micra in width were in evidence at a height of ten feet. By this date no tracheids but only swollen cells were noted at the lowest level but ten days later four layers of tracheids had been differentiated. More frequent sampling would have been of value in this analysis but one of the limitations of this method of investigation lies in the fact that the number of samples available at any one height is limited and by taking them more frequently than was done we should have run the risk of killing the tree or injuring it so severely as to make the data of little or no use. While the amount of sampling done on this tree must have been near the limit, it was not sufficient to invalidate the dendrometer readings which agree in all essentials with similar ones taken from other trees.

The curves obtained for various heights in the tree, with the exception of the ten-foot curve, corroborate the evidence secured from the other pine trees by sampling; for the curve at the highest level represents the greatest radial growth at

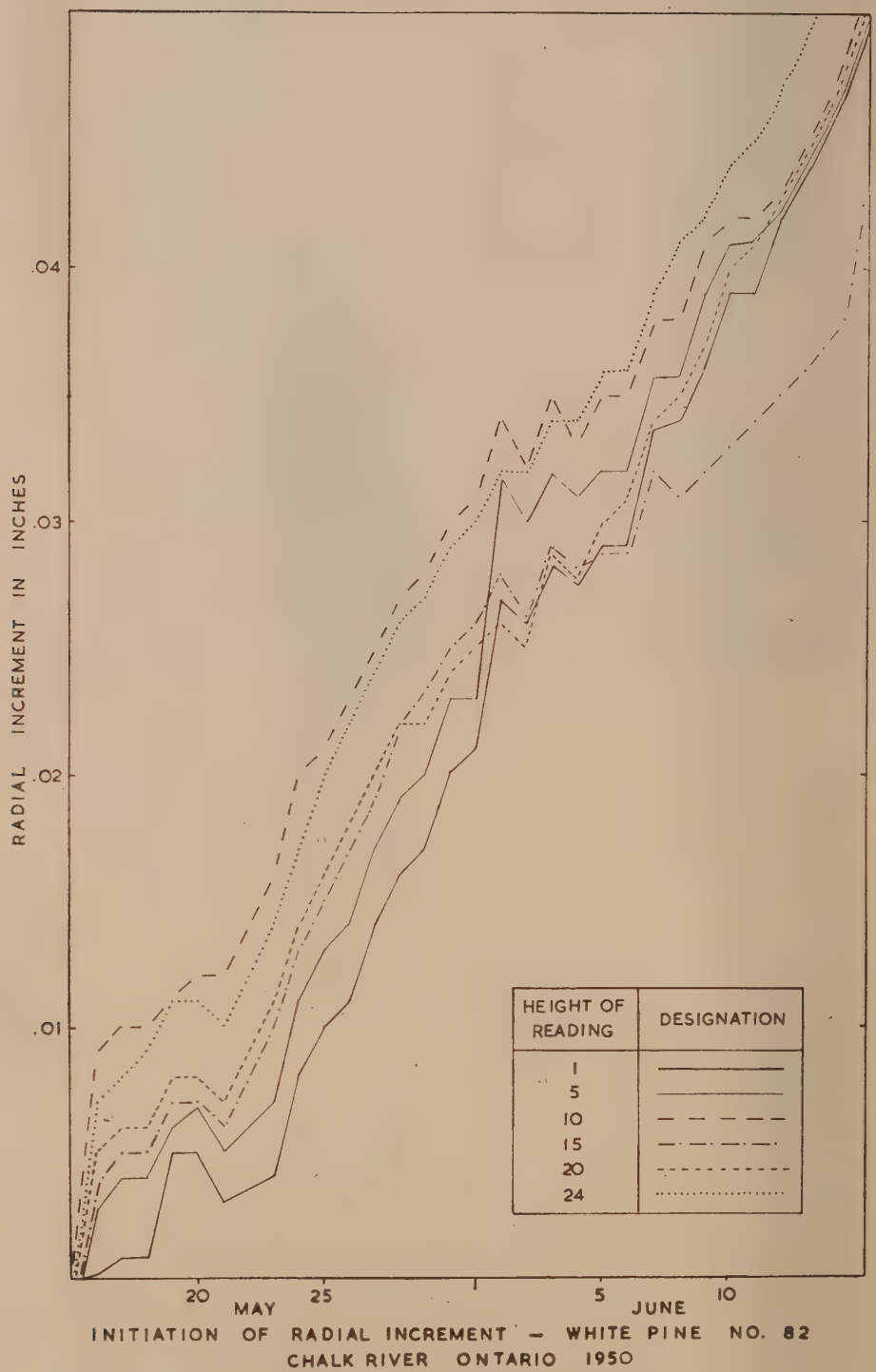

FIG. 2. Initial march of radial increment, as measured with a dendrometer, at different levels in the trunk of a weeviled white pine.

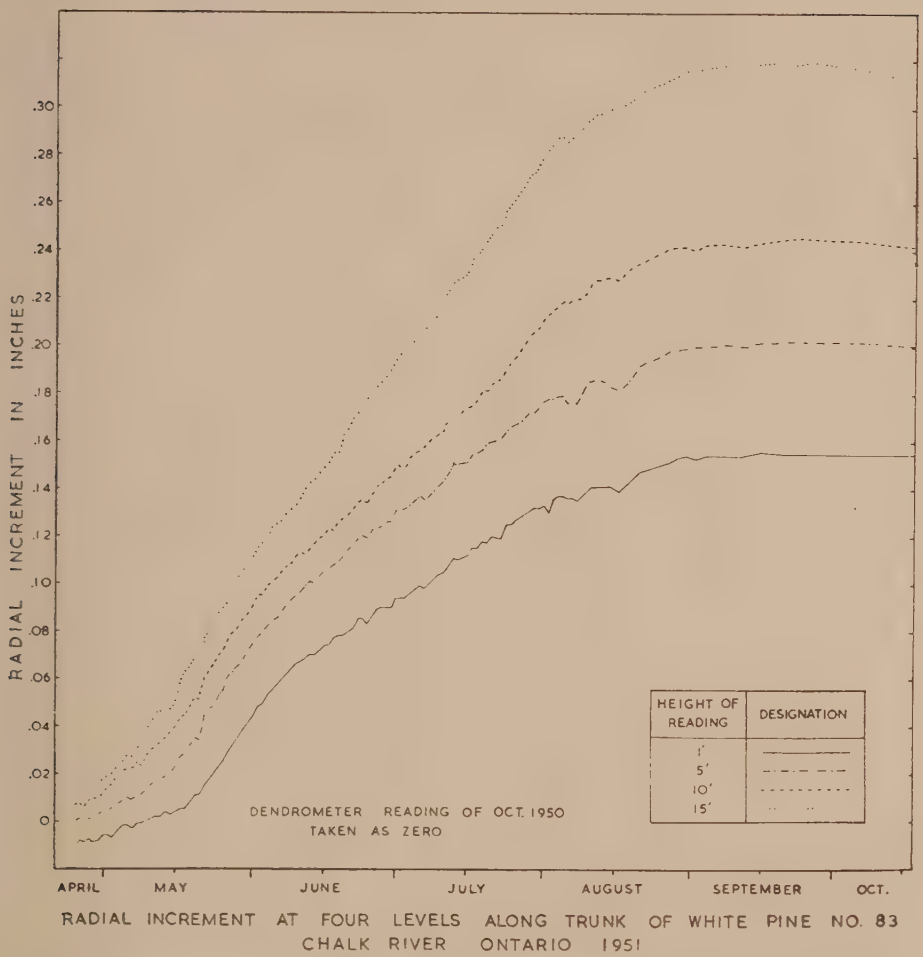

FIG. 3. Seasonal march of radial increment at different levels in the trunk of a white pine.

this time, and the others follow in proper succession and so suggest an earlier initiation in the upper regions. The ten-foot curve requires further consideration. As mentioned above, a number of strong branches extended from the trunk at this height, caused originally by the destruction of the leader by the white pine weevil. These branches were about ten feet long and each was almost as massive as the leaders extending above the 24-foot height. If, as supposed by earlier workers, the impulse to cambial activity originates at the base of the bud, it could be expected to travel along these branches as rapidly as along the leader, in which case cambial growth at the base of these branches and in the trunk at the same level would begin almost as early as at the most elevated point at which measurements were made, which in fact it did.

The fifth white pine under investigation (No. 83, at Chalk River) was 25 years old, 20 feet high with a trunk diameter of nine inches at the four-foot level. It was located 20 yards southwest of white pine No. 82, on the same site. Dendrometer measurements were made at the 15, 10, 5

and 1 foot heights as well as on the upper side of a root 18 inches from the trunk base. Records for the radial increment during 1951 growing season are shown in Figure 3. Measurements of radial increment in February 1951 indicated a decrease of some .020 inches at all levels as compared with the observations of October 1950. For this reason the 1950 October measurement was taken as zero for the graph of the 1951 records. By April 24, 1951 the 15-foot height showed the greatest increment with those of the lower levels following in regular order. The curves at all heights agree with the other trees studied in that the first permanent increment occurs at the uppermost level. The initial part of the curves represents two phases, that of swelling with hydration of cambial and bark tissue, followed by a period of cell division. Here again evidence points to the apical initiation of cambial activity.

The question arises whether this investigation can throw any light on the old problem of initiation of cambial growth in the spring. There have been no really new suggestions on this matter since R. Hartig and L. Jost, in which both held that the impulse came from the opening buds, but while Hartig believed it was caused by increased food supply, Jost held that some stimulating substance apart altogether from food originated in the buds and initiated the process of cambial activity. Doubt was, of course, thrown on both these hypotheses by the work of Brown and Knudson and their contention that cambial growth may begin in any part of the tree.

During the present study a number of trees were investigated at various heights and no evidence was found contrary to early European work. In all the trees investigated, initiation of growth proceeded from above downward or from tips of branches inward. Moreover, it has been possible to obtain good evidence as to the time of initiation and cessation of cambial growth in a considerable number of Canadian trees (Fraser 1951), and it was found in every case the annual ring was completed long before the onset of cold weather; thus Priestley's suggestion that in American trees cambial activity might be stopped by frost, and proceed in spring from the point where it left off in the previous fall, is not valid. It is therefore pertinent to inquire once again whether the concept of Hartig or Jost may not have been substantially correct.

An experiment which may have had some bearing on Hartig's theory was performed on a branch of red oak growing at Chalk River. On August 15, after the normal annual ring for 1950 was complete and cambial cell divisions had ceased, two 150-watt bulbs with reflectors were arranged so that their light shone on the leaves of this particular branch from 6.00 P.M. to 10.00 P.M. every evening, thus increasing the photoperiod to that of June 21.

The leaves on this branch remained green after the others had taken on autumn color and fallen. In fact they remained apparently in their usual summer condition, up until the time of the first severe frost of September 29. A transverse section (Fig. 4) across the pith of this branch, when treated with iodine, showed that the dark content of most of the cells consisted of stored starch. A section of a non-illuminated branch (Fig. 5), treated with iodine, indicated that the great majority of its cells were devoid of starch. It seems evident that the green leaves under artificial lighting had been producing an abundance of food and if Hartig's theory were correct one might hope to see the beginning of a new annual ring in the cambial region. Sections through the cambial regions in the two branches were examined and there was no suggestion of a renewal of growth.

After the discovery of plant hormones, Jost (1941) strengthened his theory by applying auxin to a sunflower stem and so increasing the size of the vascular bundles, presumably by increased cambial growth. Snow (1935) and later Brown and Cormack (1937) have also succeeded

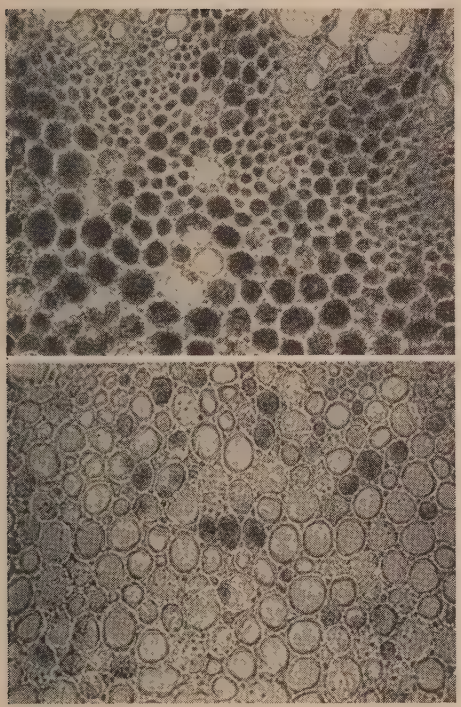

FIG. 4. Transverse section (treated with iodine) of pith of illuminated branch of red oak. The dark contents of most cells consists of stored starch. (× 30)

FIG. 5. Transverse section (treated with iodine) of pith of control branch of red oak. Very little stored starch. (× 30)

in inducing cambial divisions in severed twigs by the application of heteroauxin (b-indole acetic acid).

These results suggested an attempt to test the effect of several concentrations of b-indole acetic acid on the cambium of young pine trees. The experiments were inconclusive because of differences in the vigor of the various young trees, and also, as was learned later, by partial oxidation of the growth hormone which was applied to the trees in a lanolin mixture (Redemann, 1950). They were suggestive, however, and seemed to indicate that while greater dilutions have no effect, a concentrated one may repress radial growth, and concentration of $1/1000$ showed promise. Such a dilution was applied to the stem of fast growing seedlings of *Pinus radiata* Don. of the first year. Here the effect was unmistakable. The treated part of the stem increased to at least three times the diameter of the rest of the stem, seemingly using up the available food and preventing normal growth in length. Sections of the treated stem indicated that a considerable amount of radial increment was caused by proliferation and enlargement of the cortical cells, but the cambium had also been stimulated and produced an increased amount of secondary growth. Similar changes have been reported for white pine by Wershing and Bailey (1942).

An experiment that aimed at testing the effect of heteroauxin in the cambium of a more adult tree had interesting results. In this experiment a different method was used to provide a continuous supply of heteroauxin throughout the season. A vigorous young white pine tree was chosen with a pair of branches of apparently equal size projecting at the same height from opposite sides of the trunk. In one of these branches a hole $3/16$ of an inch in diameter was bored well into the wood, a quantity of heteroauxin crystals was inserted and the aperture sealed with grafting wax. In the opposite branch a similar hole was bored in a corresponding position and sealed with wax, but without the insertion of heteroauxin. This was done on June 30 when the cambium was fully active. On September 11 the branches were removed from the tree and preserved in a formalin-acetic acid-alcohol mixture. Blocks were later cut from the treated and untreated stems in the vicinity of the holes, embedded in celloidin and sectioned. The technique did not show the details of the cambium to advantage because shrinkage had caused partial collapse of these thin-walled cells. However, the last layers of tracheids in the treated material showed a marked difference as compared with the untreated material. They were much larger, thinner walled, and resembled typical spring wood tracheids which are normally formed earlier in the growing

season. It was noted in the untreated control branch that the last tracheids to differentiate were summer wood tracheids having a relatively narrow radial measurement, a thickened secondary wall and tangential pitting. A more complete investigation of the treated branch showed that the production of the wide-lumened spring wood tracheids did not extend all the way around the circumference of the annual ring. Rather, they were formed on each side of the wound with the heteroauxin crystals, but had not formed in the quadrant directly opposite the wound. In this latter quadrant, cambial activity had proceeded without stimulation by heteroauxin and had produced an anual ring of 1950 micra consisting of 105 layers of tracheids. The outer layers consisted of summer wood. In the quadrants lateral to the wound, the cambium had an increased number of cell divisions, producing an annual ring of 2460 micra width, with 130 layers of tracheids. Directly above and below the wound, where presumably the heteroauxin would have its greatest concentration, there was considerable amount of "redwood." It is therefore apparent that heteroauxin in the proper concentration will stimulate cambial activity and favor the formation of spring wood tissue.

Summary

In the study of cambial activity of forest trees, two methods were used: the sectioning of samples of bark and outer wood, and the daily measurements of radial increment with the dendrometer. Although the latter method gives a more continuous set of measurements, yet the sections assist in the interpretation of the results.

The contention of the early European workers, that the march of initiation of cambial activity proceeded from the apex to the base, was found to be true for trees studied in Ontario, and the suggestion that American trees might behave differently because of the cold winters was not substantiated.

Concerning the controversy between R. Hartig and L. Jost, experiments verify the latter's theory of a stimulus, not associated with food, proceeding from the buds and developing leaves in the spring, and being responsible for the apical initiation of cambial activity. This stimulus is probably produced by a growth hormone which former workers have shown to be present. The application of heteroauxin in the proper concentration stimulates cambial activity and the continued production of spring wood. With a greater concentration, "redwood" or compression wood is produced.

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NOTES AND COMMENT

NOTES ON AMPHIBIAN AND REPTILE POPULATIONS IN A LOUISIANA PINELAND AREA

Mass sampling of amphibian and reptile populations is a difficult process and is usually subject to considerable bias on the part of the collector. We believe the material presented here to be valuable in that it is less subject to such bias.

While working as members of the 1950 Tulane University Field Expedition near the town of Angie, Louisiana, the authors discovered that a ditch, dug to receive a pipeline, was trapping large numbers of amphibians and reptiles. Over a period of three days, in approximately sixteen actual collecting hours, 667 individuals of 40 species were taken from this ditch.

Angie is located in Washington Parish in the extreme northeast corner of the eastward projection of the state known as the Florida Parishes. The terrain is flat or rolling, with forests of pine and hardwood interspersed with gum and cypress in the depressions and along the stream courses. There is considerable land in pasture or under cultivation. The soil is sandy with a mixture of clay. The area is drained by the Pearl River.

The ditch ran southeast from Angie towards the river. The section from which the authors collected began about four miles from town and extended toward the river for a distance of approximately 10,380 feet. The ditch was 24 inches wide and averaged 48 inches deep. The sides were vertical and had no tendency to slide. The bottom was covered with a layer of loose earth, with lumps up to six inches in diameter, and bits of tarred paper from the pipe, which rested overhead on temporary supports. A strip about fifty feet in width adjacent to the ditch had been cleared of trees and underbrush. The ditch had been dug by a mechanical digger which deposited a ridge of dirt about three feet high along the south edge.

One of the authors discovered the ditch on June 2nd, at about 2 P.M. At this date it had been dug for two or three days. Since the bottom of the ditch was not systematically examined until June 4th many animals may have been present, but the only specimen taken was an *Ophisaurus*. A strip of forest parallel to the ditch, at a distance of about 100 yards was searched for more than half a mile and proved almost barren to standard collecting technique. Heavy rain began during the afternoon and continued most of the next day.

On June 4th the ditch was worked by a single collector from 5 to 6 P.M. and by three collectors from 6 to 7 P.M. It was found that most of the animals were overlooked if the collector walked beside the ditch and that it was necessary to walk in it, carefully raking over the debris at the bottom. By this method 263 individuals belonging to 25 species were taken in four man-hours.

On June 5th a new section of the ditch was covered by the three man crew. In order to obtain detailed notes a system was used whereby one man walked in the ditch, finding and handing up specimens to the second man who carried the sacks, while the third kept notes. The beams that supported the pipe over the ditch were approximately sixty feet apart and this interval was used as a unit for which the animals taken and the vegetation along the ditch were recorded.

Rain began on the night of June 5th and lasted through the sixth. On the afternoon of the 6th two collectors went back over the area covered on the 4th, plus a short additional stretch to the west.

Total rainfall through the period was given as 2.22 inches at Bogalusa, the nearest recording station. Temperatures were cool to moderate. Morning temperatures (8:00 to 9:00 A.M.) ranged from 25° to 29° C.

Table I shows the results of this collecting. The collections of June 4th and 6th are placed together to allow comparison.

Before further discussion of this material we must mention certain points of a systematic nature. The first pertains to the toads of the genus *Bufo*. The status of three forms, *valliceps*, *fowleri*, and *terrestris*, is difficult to ascertain in southeastern Louisiana. While typical individuals of all three can be found, numerous others show characteristics of two or even three forms, even though the ranges of *valliceps* and *terrestris* are not known to overlap. The authors have in mind no contribution to this complex problem at this time, but it was felt that some indication of the affinities of toads taken in the ditch should be given. One sample, that of June 6th, was therefore broken down on the basis of the characters given by Wright and Wright (1949).

A second systematic question is that of the dwarf four-toed salamander. After study of several collections of *Manculus* from various parts of Louisiana the authors find themselves unable to apply the recent subspecific distinctions of Mittleman (1947) and therefore give no subspecies.

The section of ditch covered on June 4th was approximately 5340 feet in length. At the western end it was bounded by a small stream known as Ord's Creek. Within 100 yards it rose from the creek bottom to the level of the

TABLE I. *Collections June 2–6*

Species / Date....	Individuals taken June 2nd	4th	6th	5th	Total
Ambystoma opacum	—	4	1	—	5
Triturus v. louisianensis	—	1	1*	1	3
Manculus quadridigitatus	—	1	1	2	4
Plethodon glutinosus	—	1	1	3	5
Pseudotriton f. flavisimus	—	—	—	1	1
Desmognathus fuscus auriculatus	—	—	1	12	13
Eurycea longicauda guttolineata	—	—	1	—	1
Salamander totals	0	7	6	19	32
Hyla avivoca	—	1	—	—	1
Hyla versicolor	—	18	7	5	30
Hyla squirella	—	5	—	2	7
Hyla gratiosa	—	3	2	1	6
Hyla cinerea	—	3	4	3	10
Hyla femoralis	—	10	9	15	34
Hyla crucifer	—	—	1	2	3
Pseudacris nigrita trisereata	—	1	2	1	4
Acris gryllus gryllus	—	20	30	22	72
Hylid totals	0	61	55	51	167
Rana grylio	—	1	—	1	2
Rana clamitans	—	5	6	5	16
Rana pipiens	—	5	10	7	22
Rana catesbiana	—	—	—	1	1
Rana palustris	—	—	1	—	1
Ranid totals	0	11	17	14	42
Bufo woodhousii fowleri	—	—	13	—	13
Bufo terrestris	—	—	33	—	33
Bufo terrestris/fowleri intermediates	—	—	10	—	10
Bufo valliceps? intermediates	—	—	3	—	3
Unidentified *Bufo* (released at site)	—	49	6	43	98
Bufo quercicus	—	5	2	5	12
Bufo totals	0	54	67	48	169
Microhyla carolinensis	—	118	55	59	232
Ophisaurus ventralis	1	—	—	1	2
Cnemidophorus sexlineatus	—	1	—	2	3
Sceloporus u. undulatus	—	7	2	3	12
Anolis carolinensis	—	—	—	1	1
Eumeces anthracinus	—	—	1	—	1
Lizard totals	1	8	3	7	19
Diadophis punctatus stictogenys	—	1	—	2	3
Haldea striatula	—	1	1	1	3
Tantilla coronata	—	—	—	1	1
Thamnophis sirtalis proximus	—	—	—	1	1
Coluber c. constrictor	—	—	—	1	1
Natrix rigida	—	—	1	—	1
Natrix sipedon pleuralis	—	—	1	—	1
Heterodon platyrhinos	—	1	—	—	1
Snake totals	0	3	3	6	12
Terrapene carolina	—	1	1	1	3
Kinosternon subrubrum hippocrepis	—	—	—	2	2
Turtle totals	0	1	1	3	5
Grand totals individ.	1	263	207	207	677
species	1	25	26	31	40

* An aquatic adult seen but not captured.

pine forest. This forest was a sparse stand of second growth longleaf pine and turkey oak. Undergrowth was scarce to nonexistent. There was little grass or other low vegetation and almost no duff or humus. The only soil cover over much of this forest was a very thin layer of pine needles and leaves. Charred stumps and tree bases indicated that the forest was subject to frequent fires which kept the undergrowth killed off and prevented the accumulation of organic matter in the soil.

On June 6th this area was rapidly covered a second time. Heavy rains had flooded some portions of the ditch to a depth of 12 inches, but there did not appear to be any increase in the possibility of escape for trapped animals. An additional 2,000 feet of ditch running through open pasture to a thin strip of woods on the west bank of Ord's Creek was covered, but was not productive and almost all of the material came from the area previously worked on the 4th. The collections of the 4th and 6th may be compared in Table I. Although the number of individuals was smaller on the 6th, more species were present. Of the nine species represented by five or more individuals on June 4th, five showed a decrease on the 6th and four showed an increase. Of the forms taken on the 6th for the first time, none was represented by more than a single individual.

Without experimental evidence it is difficult to assess the efficiency of the ditch in sampling the population, but the fact that the animals removed from the ditch on the 4th were so nearly replaced on the 6th indicates that there was considerable movement by individuals and that the local populations must have been fairly dense.

The information obtained on June 5th is summarized in Figure 1. Using the method described above we covered 50 units, or about 3,000 feet. This was broken in two places by swamps. The first was about 100 yards in width, while the second was at least ¼ mile. In the second swamp a dragline was digging a wide ditch which filled with water and trapped nothing. Numerous *Desmognathus* and a single *Pseudotriton* were unearthed, however, and were recovered from the piles of freshly deposited mud and sand. Since the ditch was not effective in capturing animals in these swamps they are not included in the total distance indicated in Figure 1. In the figure the number of individuals of a species taken are indicated by the height of the blocks. Where three or more individuals were found in a unit the number was written in. The nature of the vegetation is indicated diagrammatically and further explained by brief captions. By this method correlations between the distribution and abundance of various forms and the habitat may be shown. The validity of these correlations rests on the assumption that there was little movement along the ditch. Of the species taken, only *Acris gryllus* showed a tendency to move along the ditch to escape capture. Further, where there were breaks in the ditch and the sloping ends offered an easy opportunity for escape, no marked decrease in the abundance of trapped animals was observed. Thus, while some movement must be assumed, we do not believe it was sufficient to invalidate the correlations discussed below.

The first four units sloped to and away from the small swamp. The three species found here were all found in the adjacent pine-oak area. This latter, seven units in length, was open forest with no undergrowth except scattered shrubs and sparse grasses. It had been frequently burned over and the soil was dry and hard with little duff or humus. Seven species of hylid frogs were found here. Only *Acris* was at all abundant. Since *Acris* is usually found near water this abundance and its general distribution throughout the transect, often far from water, is noteworthy. In addition to the hylids this open forest supported a group of semi-fossorial species. In this group we include *Bufo terrestris, B. woodhousii fowleri, B. quercicus, Microhyla carolinensis* and *Plethodon glutinosus.*

The second swamp followed this pine-oak section. The vegetation in the area beyond the swamp was predominantly low second growth pine. The trees were scattered and there were patches of sumac and *Myrica* with dense grasses growing in the openings. *Microhyla* and *Bufo* were present in small numbers. *Acris* was common. *Rana clamitans* and *Rana pipiens* appeared for the first time. Reptiles, conspicuously absent from the open pine forest, were represented by a single *Sceloporus.*

Units 23 to 39 ran through open land, partly under cultivation. Of this, units 26 to 34 were in a cornfield. Beyond the cornfield were five units running through a densely grassed hayfield and the corner of a potato patch. This open land supported the most varied population of the transect. The virtual restriction of reptiles to this open ground is remarkable.

The last eleven units were in pine forest once more. This forest was different from that previously sampled. Except for a narrow burned-over belt at the edge the trees were large, tall, and close together. There was a low understory of *Acer* and *Myrica* and a good growth of grass. There was a thick layer of pine needles. The area had not been burned for a long time and a good layer of humus had been built up. The most notable features were the dense *Microhyla* population, and the common occurrence of *Hyla femoralis.*

Interpretation of these relationships requires that we consider the factors that determine the

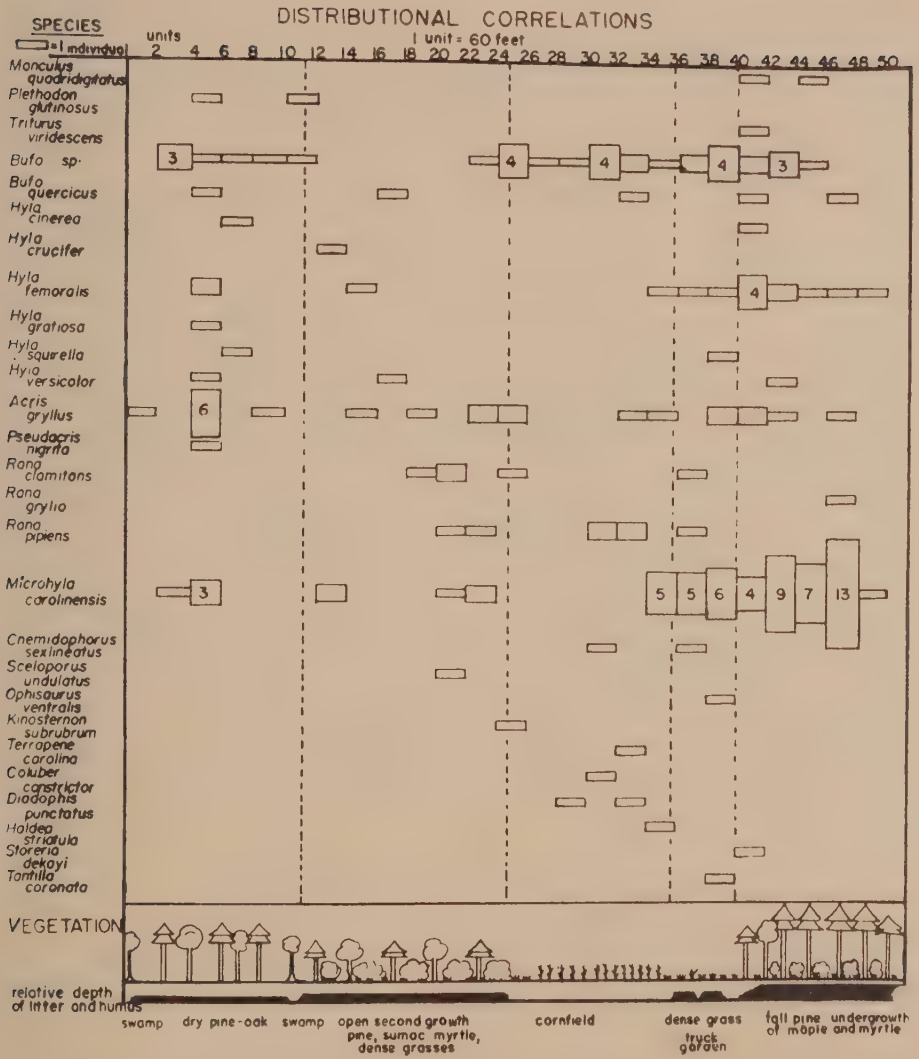

FIG. 1. The distribution and abundance of each species is indicated by the blocks to the right of the species name. Horizontally, each block represents a distance of 120 feet. The vertical dimension of the block indicates the number of specimens taken in that interval. Where three or more individuals were taken the number was written inside the block. The thickness of the black line is a very rough estimation of relative depths of the organic soil layers. The slight discrepancies between the totals indicated here and the collections of June 5th as shown in Table I are due to specimens taken in a section of ditch not covered by this figure.

effectiveness of the ditch as a collector. These include mechanical factors pertaining to the structure of the ditch; its width, depth, and the composition of the sides; environmental factors such as weather conditions; and biological factors, primarily the behavior patterns of the animals concerned. In this instance five of the species of frogs taken were in breeding congress during the study period. In addition the heavy rainfall undoubtedly encouraged amphibian movement. Some selectivity is also unavoidable. Large *Coluber* and *Elaphe* could undoubtedly cross the ditch, or escape, and the larger tree frogs would have no difficulty in

leaping across the ditch, although they were apparently unable to escape, once trapped. Movement within the ditch we believe to have been slight.

Conclusions

1. The ditch provided, on the whole, a highly efficient collecting place and as such served as an excellent transect of a number of typical pineland environments.

2. Collections over the same stretch of ditch, two days apart, indicated a dense population and considerable degree of movement for many species.

3. Carefully annotated collections from another portion of the ditch suggested significant correlations of faunal distribution and density with vegetation and soil conditions.

4. The efficiency of the ditch as a collector contrasted sharply with that of standard collecting techniques. In an area found very unproductive by ordinary methods high and varied populations of amphibians and reptiles were found to be present. The difficulty of obtaining accurate population and distributional data from ordinary collecting is emphasized.

In addition to the above conclusions the experience gained in collecting and studying this material shows that ditches of this type offer invaluable opportunities for population study. For full utilization of these opportunities, however, techniques must be at hand for the analysis of certain vital factors. In the hope that we will chance upon similar situations in the future we have prepared a brief outline for such an approach. This outline consists of two main portions, as follows:

I. Determination of basic data.
  A. Accurate and detailed weather records at the site.
    1. Hourly readings of temperature, rainfall, relative humidity, evaporation rate, and light intensity.
      a. Correlation of these readings with hourly collections would provide excellent data on time and conditions of movement for various species.
  B. Application of standard methods of vegetational analysis and soil sampling.
II. Determination of the range and accuracy of the ditch as a sampling tool.
  A. Range and degree of effectiveness determined by release of marked individuals.
    1. One alternative is collecting, or strip censusing, parallel to the ditch. This raises a difficult problem of habitat disturbance. If enough data are available a statistical compensation might be possible.
    2. A second alternative is use of a system of tarpaper drift fences and funnel-type traps. By this method habitat disturbance can largely be eliminated and a good number of individuals can be marked and released in a short time. Tattooing with a portable electric outfit is probably the best marking technique for this work.

The authors wish to thank Edward Peebles of Tulane University for aid in subspecific identification of *Acris gryllus* and Fred R. Cagle for helpful criticism of the manuscript.

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A METHOD FOR CONTROLLING NATURAL SOIL TEMPERATURE GRADIENTS

In attacking the problem of the effect of surface temperature of certain barren soils upon seed germination and seedling establishment, it was desirable to implement field studies with controlled laboratory experimentation. For this purpose a method was devised for obtaining controlled soil temperature gradients which equal those occurring in the field. This method, with modifications, is applicable to a variety of soil-plant temperature relationship studies other than the one mentioned here.

Data obtained by this method indicate that radiant energy from infrared lamps, when striking the surface of the soil, is distributed below the surface in a manner similar to that of radiant energy derived from insolation. Thus, if the surface temperature is controlled, the soil temperature gradient is likewise controlled in a way similar to that obtaining in nature. Factors described by the inverse square law prevent duplication, by this method, of naturally occurring temperature gradients in air and plants im-

mediately above the soil surface. Gradients that do occur, however, can be controlled and are useful when (1) temperature effects are desired at only one level, as of a bud or a leaf, and (2) when the plant structures are at about the same level as the soil surface, as seedlings or emergent buds from sub-surface perenniating stems and root stocks.

A diagrammatic representation of an inexpensive and easily asembled apparatus used for this method is given in Figure 1. The frame (A), is a photographic enlarger stand. The

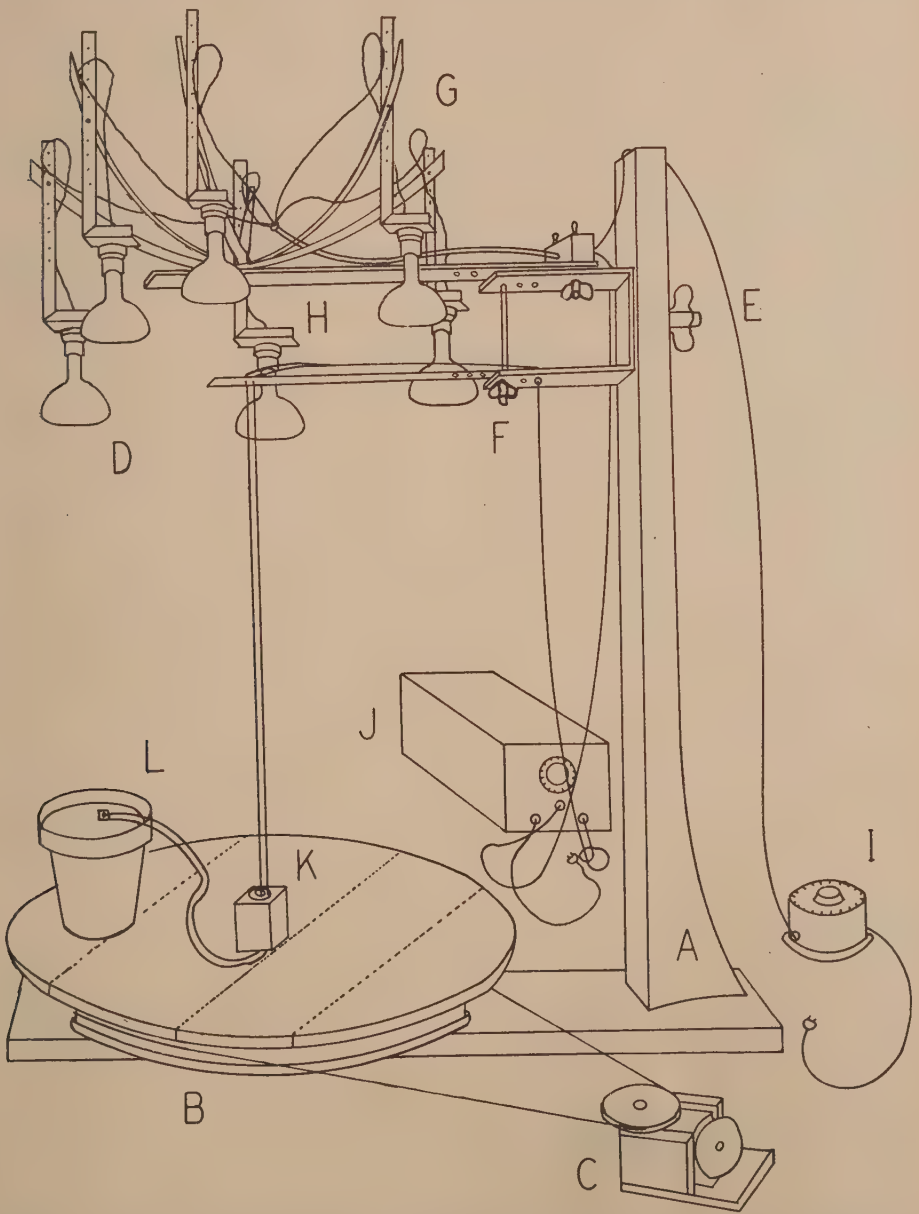

FIG. 1. Apparatus for the production of controlled soil temperature gradients. Explanation given in text.

turntable assembly (B), capable of easy rotation under heavy weight, consists of a wooden platform mounted on a complete front wheel assembly of a car secured from a junk yard. The assembly should be selected from a car in which the axle is so constructed that, when cut off by the junk yard attendant with an acetylene torch, it will serve as a flat base upon which the wheel revolves. The wheel is rotated at 3 r.p.m. by a belt passing around the wheel rim to a pully of a constant speed reductional gear motor (C). The battery of six reflector type (General Electric R-40) infrared lamps of 250 or 375 watts (D) may be moved vertically by means of an adjustment (E), and horizontally by another (F). Each lamp may be swung in or out and moved vertically by an adjustment (G), and may be moved horizontally by a center one (H). Heat intensity is controlled by a Variac (I), as well as by lamp position.

A thermal control unit, with a sensitivity of 1°C, was designed and built by the junior author. Its components are a Thyratron switching circuit (J), a mercury well contact (K), and a Western Electric disc type thermistor used as the temperature sensing element (L). Since experience demonstrated that surface temperatures in relatively still air could be accurately controlled by regulation of lamp position alone, use of the Thyratron control unit was discontinued.

All experiments with this apparatus were carried out in a greenhouse where the factors of air temperature, humidity, and light intensity could be regulated to approximate those naturally occurring. Soil water content was controlled by the use of water baths around the soil containers. Lamps and soil containers were adjusted so that the soil surface area to be studied received an even distribution of radiant energy. With six lamps it was possible to heat effectively surface areas ranging up to 8 inches in diameter, when placed on the outer circumference of the platform and rotated at 3 r.p.m. By use of additional lamps, greater areas can be covered. Since surface temperatures are constant for a given set of lamp positions and intensities and soil conditions, the details for a particular experiment need be worked out only once. For the apparatus here described, a working distance from lamps to soil surface of 10 to 30 inches was found to be adequate for surface temperatures of 30° C to more than 80° C. By placing each of several pots at different elevations above the turntable, several temperatures throughout this range were obtained simultaneously.

Since large temperature fluctuations occur within small spatial limitations on and near the surface, use of very small temperature sensing elements, such as thermistors or thermocouples, is desirable. All such temperature determinations for this work were made with a Western Electric Model D170575 bead type thermistor, capable of registering variations of 0.01° C within 0.4 mm. spatial limitations (Platt and Wolf 1950). For soil temperature determinations at depths of more than one inch, both mercury bulb and metal dial type thermometers were used. The latter, though easier to use, is less accurate for a specific depth in that its elongated sensing element indicates an average of the temperature conditions existing over an inch or more in depth.

The described apparatus was used successfully by the senior author over a five month period in 1947.[1] During this time more than 60 experimental "runs," varying from a half hour to eight hours in duration, were made on a variety of soils and plants. Representative data obtained on one soil are presented in Figure 2.

Several additional aspects of this problem were developed by the senior author during the summer of 1951. An improved model of the temperature control device was secured through funds made available by a Grant-in-Aid from the Research Committee of Emory University. The turntable was enlarged to a diameter of five feet and reinforced with steel so as to support containers weighing several hundred pounds each. The lamp to turntable distance was increased to four feet. Twelve lamps were provided, with eight of them controlled through the Variac (the maximum number of 250 watt lamps the V-20-M model can handle), and the other four controlled with an on-off switch.

The open circular mercury well used as a contact between the turntable and frame for the temperature indicating circuit was abandoned. Instead permanent binding posts were installed with the current between them being conducted through copper slip rings and G.E. dual brush holders equipped with self-cleaning wire carbon brushes. This arrangement eliminates temperature effects of the mercury pool and errors in resistance contacts due to oxidation and the presence of foreign matter in the mercury. The positive contacts also reduce contact resistance. The use of multiple contacts is simplified by increasing the number in this model to three.

A General Electric Type DW-68 sunlight radiation meter (ca. $40.00) provides an easy and inexpensive means of adjusting this device to desired radiation intensities, and as well provides a means for the determination in the field of radiation intensities for stated conditions of season, latitude, slope and exposure. The sensing element of the meter, a radiation type vacuum thermocouple, has a response range of 300–

[1] Facilities and funds for this part of the investigation, carried out in 1947–48, were provided by the Department of Botany of the University of Pennsylvania.

3500 millimicrons and a sensitivity of 0–2 gram cal./sq. cm./min. Conversion factors for other scales are provided.

Byram and Jemison (1943) devised an "artificial sun" for studying the effect of radiation on forest fuel moisture under a variety of topographic and atmospheric conditions, somewhat similar to the one described in this paper. Although the range and versatility of their instrument is much more restricted, it does possess the significant advantage of including wind as a second variable. The device consists of a rec-

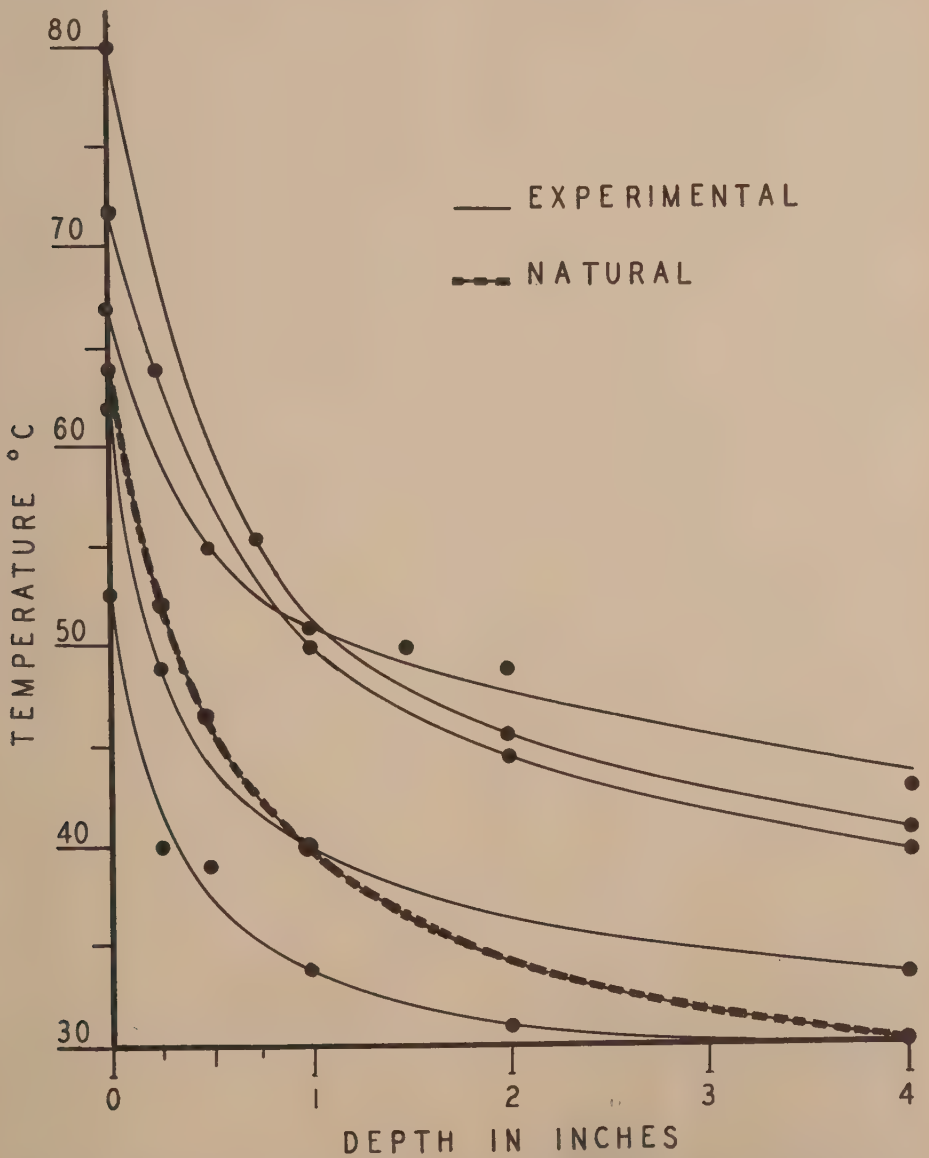

Fig. 2. Representative temperature gradients determined for a rocky silt loam, placed in six-inch pots under varying radiant energy intensities and soil moisture conditions. Temperatures plotted are the maxima obtained for each level. Methods for temperature determination are given in text.

tangular wooden box divided by a horizontal glass sheet into upper and lower compartments. The lower and shallower compartment, open to the ground and at both ends, serves as the experimental chamber and as a wind tunnel. The upper compartment, containing twelve 150-watt tungsten bulbs arranged on the perimeter of a circle, provides the source of radiant energy. The problem of uniform distribution of energy is very neatly solved. Quoting the authors, "It has been shown mathematically that a circular source of light or radiation gives uniform distribution of energy on a surface parallel to the plane of the source and situated at a distance from that plane equal to the radius of the circle. As the radius in this case was nine inches, the bulbs were so placed that they were separated by a space of nine inches from the leaf litter or other fuel tested." (This method cannot be applied with the reflector type bulbs used in the apparatus described above.) Wind velocity was varied by adjustment of the electric fans used in the tunnel, and intensity of radiation was varied by turning on or off some of the bulbs evenly spaced in the circle. Especially designed ice calorimeters were used to measure intensity of radiation.

Theoretical and practical discussions of solar radiation of particular significance to the kinds of problems suggested in this paper have been given by Byram and Jemison (1943) and by Geiger (1950).

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THE SPREAD OF THE ARMADILLO IN FLORIDA

The nine-banded armadillo, *Dasypus novemcinctum texanum* Bailey, is now common in many parts of Florida, and apparently is extending its range in that state. The rapid spread of this introduced mammal is of considerable interest, and merits the attention of ecologists.

Armadillos have appeared at scattered localities in Florida for many years. Most of them were thought to have escaped from captivity. Even as late as 1943, Hamilton (1943) considered Florida records to have been based on escaped examples, although Sherman (1943) indicated the species to be established in the eastern part of the state, between the St. Johns River and the coast.

In 1922, an armadillo was caught near Miami, Dade County; and in 1924, a female with young was killed in the same area (Bailey 1924). Also in 1922, two armadillos were noted at Williams Point, in Brevard County; they were thought to have been a pair that escaped several months before near Cocoa. Another armadillo is known to have escaped near Cocoa about 1924.

An armadillo was killed at Flagler Beach, Flagler County, in 1934, and one was caught at Titusville, Brevard County, in 1936. In 1938, the species was reported six miles south of Indian River City, Brevard County, and near Crescent City, Putnam County. In 1941, it was known from Pinemount, Suwannee County; and in 1943 a specimen was found in South Jacksonville, Duval County. All these records, except the Suwannee County one, were east of the St. Johns River.

Sherman (1943) summarized the previous records and added new ones. He concluded that the armadillo was well established in four adjoining counties (Brevard, Volusia, Flagler, and Putnam), east of the St. Johns River. Additional records for Flagler and Putnam counties were provided by Moore (1946) and Pournelle (1950).

Newman (1949) discussed the spread of the armadillo. Available to him were reports of game wardens throughout Florida. He concluded that the species was established in Brevard, Volusia, Flagler, Putnam, St. Johns, Indian River, St. Lucie, Martin, Okeechobee, Osceola, Polk, Orange, Seminole, and Lake counties. In addition, he presented scattered records for Hamilton, Alachua, Marion, Sumter, Pasco, Manatee, Hardee, De Soto, Lee, Hendry, Palm Beach, and Broward counties. He considered these scattered records to have been based merely on escapes from captivity, but offered no reason why the state should suddenly

break out with a rash of escaped armadillos. The distribution of these records, to my mind, strongly suggested that the animal was radiating out from the eastern part of the state, where it was known to be firmly established.

In 1951, I made collecting trips to many parts of Florida, and saw large numbers of armadillos, both living specimens and highway casualties. The animals were extraordinarily abundant in Volusia and Brevard counties; often six or seven would be seen dead on the road in a half-mile stretch. The creatures had reached some offshore islands; I saw one on the wooded northern portion of Merritt Island, six in the orange groves of southern Merritt Island, and one a little south of Cape Canaveral. Specimens were also noted in Duval, St. Johns, Flagler, Putnam, Broward, and Dade counties. About 50 armadillos were seen in the central portion of the state, in Polk, Lake, Sumter, and Marion counties. Scattered specimens were observed in Pinellas, Hillsborough, Pasco, Hernando, Citrus, Levy, Dixie, and Taylor counties, on the west coast; and in Wakulla County, in the Panhandle. No trips were made to the western portion of the Panhandle. The 1951 records are shown on the accompanying map (Fig. 1).

It should be emphasized that I did not reach

FIG. 1. Spread of the armadillo in Florida. Hatched areas, range of the species in 1943, after Sherman. Stippled areas, range in 1949, after Newman. Solid symbols, author's records in 1951.

many parts of the state, and that I made no special effort to find armadillos, but merely kept records of those seen.

Evidently the range of the armadillo now blankets Florida, with the exception of the swampy southwestern portion of the peninsula, and the possible exception of the western Panhandle. This remarkable spread has taken place certainly in the last thirty years, and probably in the last twenty.

Apparently, the armadillo first became established in Florida along the upper east coast. Some residents of this area claim that the original introduction took place near New Smyrna, Volusia County, in the early 1930's. Today the species is excessively common there; local youths may catch a dozen in a night's hunting. However, Sherman (1937) indicates the possibility of an introduction at Cocoa, Brevard County, about 1924.

The armadillo now frequents numerous plant associations in Florida. It is often seen in turkey-oak and longleaf pine; rosemary scrub, both coastal and inland; abandoned fields, especially those overgrown with broom-sedge and dog-fennel; and the drier parts of slash pine and wire-grass flatwoods. It is somewhat less frequently encountered in mesic hammock and live-oak hammock. In addition, it commonly invades orange groves, tung orchards, gardens, and cultivated fields. Occasional armadillos forage in hydric hammock and about the borders of ponds and lakes. (See Carr 1940 and Laessle 1942 for descriptions of plant associations in Florida).

Newman's 1949 paper merits discussion. This author was then Director of the Florida Game and Fresh Water Fish Commission, and his article appeared in the Commission's magazine. It reflected the "official" viewpoint at that time, and is therefore of considerable interest. Newman contended that the armadillo did no harm, and that in fact it was to be welcomed because it fed mainly on insects and had potential food value to man. However, these contentions were based on observations made in Texas; the habits of the species in Florida were not studied. It is interesting to note that Fitch (1949) considered the armadillo to have been an important predator on insectivorous lizards in Louisiana.

The armadillo has proven most undesirable from an economic standpoint. An editorial in the *Orlando Sentinel* (March 18, 1951) summarized public sentiment concerning the animal in Florida: "This destructive creature has grown in numbers to such an extent that grove owners are up in arms in protest against the armadillo depredations in the [orange] groves, where their burrowing proclivities fill up the ditches with their excavations. Nurserymen will tell you that a single armadillo that gains entrance to a slat house or [to] beds where tender plants are coming to maturity [can do] thousands of dollars of damage . . . in a single night. Hunters claim that the armadillo is very devastating to quails' eggs." Many Floridians state that their flower or vegetable gardens have been uprooted and destroyed by armadillos.

Summary

A few armadillos, supposedly escapes from captivity, were reported in Florida in the 1920's. In the 1930's or perhaps a few years earlier, the species was introduced along the upper east coast of Florida. By 1943 it was well established in four eastern counties. By 1949 it was known to be common in fourteen counties, and there were scattered records for twelve other counties where it probably was established. By 1951 the species ranged throughout the state, with the exception of the swampy south-western portion of the peninsula and the possible exception of the western Panhandle.

The armadillo has invaded many plant associations in Florida. It is regarded with disfavor by many local residents, and especially by those engaged in agricultural or horticultural pursuits.

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AUTECOLOGICAL STUDIES OF IMPORTANT FOREST TREES [1]

In 1946 at the Boston annual meeting, D. B. Lawrence proposed that the Ecological Society of America publish a series of carefully selected ecological life histories of native plant and animal species. The then President Aldo Leopold appointed a committee to look into the proposal. Soon after the establishment of the committee, the point of attack shifted from setting up an elaborate program of publication to a program of pointing out what needs to be done in this field of research (Lawrence 1948). Foresters familiar with the activities of the Ecological Society received this emphasis with more than usual interest since ecological life histories of trees have a great deal of significance to them. In fact, for many years, foresters have been concerned with studies of economically important forest trees which have approached in greater or lesser degree, the ecological life history. While few of these studies are complete in themselves such investigations as those undertaken by Isaac (1938, 1943, 1949) on Douglas fir, by Haig (1936) and Haig et al. (1941) on western white pine and associated species, by Munger (1917) and Pearson (1923, 1942, 1950) on ponderosa pine, by Chapman (1926), Gemmer et al. (1940), and Wahlenberg (1946) on longleaf pine and by Korstian (1927) on oaks, are contributions toward ecological life histories which are of considerable significance. Moreover, the investigations of ecologists on trees of importance in forestry such as those of Clements (1910) on lodgepole pine and Cooper (1917) on redwoods, have practical significance and immediate application in forest practice. Pelton (1951) has provided a distinct service in outlying life history studies of woody plants.

One of the problems with which the forester is concerned and with respect to which ecologists can give him major assistance is that of obtaining natural reproduction of the desired species. No phase of silviculture presents more complex or critical problems than the general field of natural forest regeneration. The traditional approach most commonly used in forestry is experimental, in which a number of different methods of cutting are applied to particular stands with the objective of determining which is most successful in obtaining natural regeneration. However, the types of cuttings to be made and the variations to be applied can be ascertained most satisfactorily if a thorough background on the autecology of reproduction of the desired species is available. Such life history information may also have other practical implications of value to the practicing forester. For example, it might help in a breeding program aimed toward improving the genetic makeup of a particular tree, or it might assist in determining whether a given site is suitable for planting a particular species. Species not yet thoroughly studied on which reproduction research would be highly desirable include: eastern white pine; sugar pine; red pine; shortleaf pine; loblolly pine; slash pine; Sitka spruce; redwood; northern white-cedar; western redcedar; Port-Orford-cedar; Alaska-cedar; black walnut; yellow birch; beech; yellow-poplar; sugar maple; and basswood.

To be of greatest significance, research in the field of forest reproduction should be concentrated upon those factors and within those limits found in the natural environment. The results are then realistic and will have more than theoretical interest in that they may be applied, in silvicultural practice. One of the first points requiring investigation thus becomes the environment within which the species is found, with particular concentration upon these elements of the environment which affect the reproductive processes.

Initial investigations directed toward determining which factors in the environment are most significant in their effect upon regeneration must also be directed toward a determination of the range within which each operates. This is most easily applied to the physical factors of the environment such as temperature, moisture, and light. The biological factors are less easily assessed. Several years may be required to determine which of the many factors which may exert some influence are of major importance and to delimit the extremes in the natural range of each of these. One year may suffice to determine the approximate ranges within which some of the most obvious factors operate, although to measure each requires many years of careful observation and of selective collection of data.

Following the analysis of the existing environment, it is desirable to bring each significant factor into the laboratory where that is possible, as it often is not, and there to analyze its effect upon the organism under controlled conditions for each of the other factors. These other factors should be maintained at levels consistent with those found in nature implying more or less regular periodic variations of such factors or, less commonly, maintenance at a constant or nearly uniform level. In order satisfactorily to control all significant factors aside from that being studied, especially designed apparatus may be required.

Some significant studies may be made in the natural environment where only one important factor is artificially varied to the extent that it

[1] Published as Scientific Journal Series Paper #2704 of The Minnesota Agricultural Experiment Station.

becomes appreciably limiting. Such investigations may be undertaken only in selected areas and these areas must be as nearly comparable with respect to other significant factors as possible. In studies of this kind, the most important area for investigation of the variable factor lies within that range which is found in nature, although it may occasionally be desirable to extend the study beyond natural limits to emphasize the influence of extremes.

Following analysis of the results of controlled study of the various significant factors, additional field observations based on more complete understanding will prove profitable. The effects of interaction may be complex and may involve more than simple summation. Such synergistic relationships, although frequently important, are often of great complexity requiring large quantities of experimental data for sound statistical analysis.

To be most useful in application as in silviculture, or in any other phase of economic biology, an additional step is needed. Having measured the influence of the significant factors as they vary under natural conditions and determined the optimum ranges for each, practical questions arise: Which of the management possibilities that are economically feasible most nearly provides the requirements of the optimum environment? Which are obviously impractical, either because they fail to provide the required environment or because they are not possible economically? Where can reasonable compromise be effected between the biological optimum and the economically desirable? These questions obviously involve not only analysis of the ecology of the organism, but also thorough consideration of the economic utilization of the organism, its importance to man and his willingness to make the effort necessary to provide the required environment. It also requires an understanding of the standard as well as the less common methods of management of the organism under consideration and of other ecologically similar organisms.

The experimental work relating to actual application in forest management is perhaps best undertaken by foresters but this should be based on autecological studies provided by ecologists. Studies of this type by ecologists will serve a dual purpose: they will have scientific interest and, with the cooperation of the research forester, economic significance as well.

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OUTLINE FOR ECOLOGICAL LIFE HISTORY STUDIES OF MARINE MAMMALS

Definitions

Marine mammals are a fraternity whose members have little in common except their salt-water environment. Arising from distantly related terrestrial stocks, they have attained through parallel evolution certain superficial resemblances in anatomy and behavior. Listed in systematic order their Recent representatives include:

Order Cetacea
- Suborder Odontoceti, toothed whales
  - Family Platanistidae, river dolphins
  - Family Ziphiidae, beaked whales
  - Family Physeteridae, sperm whales
  - Family Delphinidae, dolphins and porpoises
  - Family Delphinapteridae, beluga and narwhal
- Suborder Mysticeti, whalebone whales
  - Family Rhachianectidae, gray whale
  - Family Balaeonopteridae, furrow-throated whales, or fin whales
  - Family Balaenidae, smooth whales, or polar whales

Order Carnivora
- Suborder Fissipedia
  - Family Mustelidae, weasels and allies, including a single marine member, *Enhydra lutris,* the sea otter
- Suborder Pinnipedia, seals and allies
  - Family Otariidae, eared seals
  - Family Odobenidae, walruses
  - Family Phocidae, earless seals

Order Sirenia
- Family Dugongidae, dugongs, Steller sea cow
- Family Trichechidae, manatees

At several points along the line of demarcation between marine and freshwater mammals certain species from one group invade the domain of the other. Thus, the dolphins of the family Platanistidae are typically freshwater, most of them living the year 'round in rivers and lakes of India, South America, and China. The beluga (Delphinapteridae) and several porpoises of the family Delphinidae leave the ocean at times and swim for hundreds of miles upriver. Seals of the family Phocidae are represented in Siberia and Canada by certain land-locked forms. All of the living sirenians are associated with fresh water at one time or another in their life history, and some of them are completely divorced from the sea. (The Steller sea cow, *Hydrodamalis stelleri,* exterminated in the 18th Century, was the only Recent sirenian of purely marine habitat.) On the other hand, at least two *land* mammals, the polar bear (*Thalarctos maritimus*) and the Cape Horn otter (*Lutra felina*), habitually enter the sea. We exclude these from the category of typical marine mammals on the somewhat arbitrary grounds that they are closely linked genetically with land species.

Marine mammals are distinguished by adaptations of body to an environment which is *fluid,* of relatively *cool and uniform temperature,* and *saline.*

Adaptations to a fluid medium. Body large and buoyant, ranging in size from 45 pounds in the female sea otter to 120 tons in the blue whale; usually torpedo-shaped; one or both pairs of appendages modified as flippers; with ability to withstand water pressure at great depths (the sperm whale, 3,000 feet and more); with ability to reduce oxygen consumption and to tolerate high concentrations of nitrogen and carbon dioxide while submerged (some whales over an hour). Matthews (1948, pp. 5–7) gives an expert summary of the respiratory function in whales. The myoglobin of the muscles is exceptionally rich; the muscles are able to function anaerobically for a time; the blood circulation is short-circuited during diving through a spongy network in the neck and thorax; the lungs collapse and their nitrogen does not readily find its way into the blood stream, where it would cause "caisson sickness."

Adaptations for temperature control. Body with insulating devices including blubber, or fur, or both. (The blubber also serves as a buoyant device and as a food depot.) While marine mammals range from the equator to within a few hundred miles of the poles, most of them live in cool water. Many have lost the ability to adjust readily to extremes in temperature and they may suffer when it changes. Thus, manatees died during a cold period in Florida (Cahn 1940). Alaska fur seals on land during warm, sunny weather show signs of distress,—shedding tears, drooling, and waving flippers.

Adaptations to a saline medium. Most marine mammals habitually feed below the surface of a medium which is a fairly concentrated solution (3.5 per cent) of salt. In so doing they can not avoid taking salt water into the buccal cavity. In addition they may feed upon organisms, especially invertebrates, which are saltier than the foodstuffs ordinarily ingested by land mammals. Introducing a report on their study of dolphins, Fetcher and Fetcher (1942) state that "questions regarding the mechanism by which marine mammals maintain the body salt concentration at a level scarcely higher than that of terrestrial mammals, have been raised by a

number of authors. All of the several estimates concerned with this problem . . . agree that marine mammals feeding on teleosts and other mammals are assured of sufficient water from their food at a low enough salt concentration to require no other osmotic organ than the kidney." The authors conclude, however, that marine mammals living on invertebrates may have special salt clearance devices. The kidney of a whale, for example, is divided into nearly 6,000 reniculi, each with its own blood supply. We feel that the question is far from being answered as yet, though the evidence is swinging in favor of the view that the water balance of marine mammals is no more ingenious than that of land mammals.

Reasons for Studying

To save threatened species from extermination. Marine mammals have long been pursued by man for their oil, fur, leather, and meat. The California sea-lion was once slaughtered for its genitalia alone (Bonnot 1929)! The Steller sea cow was wiped out 26 years after its discovery in 1742 (Stejneger 1886). Certain insular populations of other sirenians, as well as fur seals, elephant seals, and monk seals, have disappeared (Allen 1942). There are no North American laws protecting dolphins and porpoises. At the insistence of fishermen, bounties hang over the heads of harbor seals and sea-lions. Ownership of migratory species of Atlantic and Pacific seals is a provocative question among students of international law. On the eve of execution the larger whales have apparently been pardoned, and, since the whaling agreements of 1935 and 1948, have been well protected by the major nations of the world (Lillie 1949). Life history studies of marine mammals help to support legislation which preserves the very existence of these animals.

To establish grounds for rational use. Man is increasing in numbers and is growing hungrier, while the wise harvesting of certain marine resources is lagging behind. Whaling ships are now penetrating to the limits of navigation in the Antarctic ice. What can be done, for example, to utilize the Weddell and crabeater seals, collectively the most numerous of all pinnipeds, in Antarctica? Is the North Atlantic fishery for harp and hooded seals cutting dangerously into the capital stock? (Probably not, although present methods are wasteful and in need of improvement.) How can we achieve a balance in the numbers of harbor seals, sea-lions, and fur seals with reference to their fish-destroying habits on the one hand and their revenue-producing assets and esthetic values on the other? Why have not the Aleutian sea otters, locally abundant, extended their range during forty years of protection? Are they ready to be cropped? (And, though it is somewhat beside the point, can the manatees of Florida, the sea otters and sea-lions of California, and the porpoises of Southeast Alaska be maintained as natural wildlife resources on the strength of their esthetic or "tourist" appeal alone?)

Biologists have learned to manipulate fishery stocks, like those of the Pacific halibut and the Atlantic haddock, for the good of mankind and are slowly learning to handle populations of big-game and furbearers toward the same end. Marine mammals occupy an intermediate position, neither "fish nor flesh." Researches into the relationship between size of harvest and rate of population recruitment in the seal and whale fisheries offer a challenge to the ecologist.

To add to the fund of human knowledge. Aside from the intent to use information disclosed in the study of marine mammals for purposes of conservation and exploitation in the near future, there are non-economic (perhaps we should say cultural) reasons for wanting to find out more about them. To date, perhaps 90 per cent of all studies of marine mammals have been in the special fields of comparative anatomy, embryology, fossil history, variation, distribution, and physiology. The other 10 per cent includes life history studies of individual species. Here is the area upon which emphasis should increasingly be placed if we are to understand the marine mammals. In other words, the present need is for year 'round, birth-to-death studies of selected marine species,—studies based on the patient accumulation of data from the field as well as the laboratory.

Program of Study

Marine mammals differ from land and freshwater mammals more in degree than in kind. Thus Taylor's (1948) outlines for the study of mammalian ecology and life histories may, in their broader aspects, be used for marine as well as land forms. By way of emphasis, however, we shall list certain topics that seem to be especially important, or pertinent, to marine mammals.

Movements. The over-all range; paths of migration; movements with relation to tide, seasonal currents, and time of day; extensions of range in response to gradually warming climate and ocean temperatures; relation of range to ice movements; distribution by age and sex groups; massing or rafting of animals by hundreds on rare occasions; possibility of interbreeding with adjacent species; accessibility to hunters at various seasons; evidence of migration based on superficial body growths such as diatoms, barnacles, and seaweeds; changes in range in historic and prehistoric times; census methods, especially aerial photography and tagging; migration and international implications; local versus national jurisdiction over coastal species.

Reproduction. Time and place of birth; number of young; sex ratio; gestation period; size and growth rate of young; disparity in size of sexes; family life; how long the young are cared for (as may be two years in case of walrus); age at sexual maturity; percentage of successful breeders and percentage of successful deliveries; courtship; polyandry, promiscuity, or monogamy; territoriality; copulation; early history of the zygote (*e.g.,* delayed implantation); evidence from corpora lutea of past pregnancies; fetal development; cryptorchids and other anomalies.

Mortality. Age composition of the population as determined by sampling and by anatomical evidence of age; longevity; mortality rates by sex and age classes; parasites, including ectoparasites and tolerated guests such as barnacles on whales and seals, and diseases; fighting, trampling, drowning, crushing and suffocation in ice; deaths at birth; severe weather; predators such as the killer whale, sharks, and man; paralytic shellfish poisoning; effects of mortality factors on the species; degree and rapidity of recovery from epizootics if they exist.

Food habits. Kinds and amounts consumed, by time of day, season, and place; in the aggregate whether beneficial or harmful to mankind; food habits in relation to international interests (see distribution); food in relation to age and length of nursing period; drinking habits (do marine mammals "drink"?); behavior associated with food getting.

Environment. Temperature of the sea and tolerance limits of the species under surveillance; temperature barriers in relation to migration; seasonal currents and food supply; gradual changes in currents over a period of years; industrial pollution of inshore waters; shifting of ice masses; effect of storms on young animals on the breeding grounds and at sea; general study of environment in connection with the possibility of transplanting animals (*e.g.,* sea otters). Ekman (1935) discusses marine zoogeographic provinces.

Methods and Equipment

(We have had no experience with sirenians and are reluctant to suggest methods for studying them. It seems likely, though, that certain of the techniques listed below for the study of cetaceans, pinnipeds, and the sea otter, would also be applicable to them.)

Methods. One of the best ways to obtain information on a marine mammal is to follow the commercial industry of which the animal is the source of raw material, provided that there is such an industry. Our present day knowledge of the whales, fur seals, hair seals, and sea-lions is derived from observations made by biologists aboard hunting vessels and at processing plants. The bounty system, while generally discredited, has also provided specimens of seals and sea-lions for study. On arctic and antarctic expeditions the seals killed as food for sledge dogs have served secondarily for the advancement of science. One reason why the life histories of the sea otter and the smaller cetaceans are so imperfectly known is that these animals have not been cropped during the modern era of scientific inquiry. (An experimental harvest of sea otters in Alaska is planned for the near future. Soviet scientists have apparently pioneered in the study of sea otters but their findings are largely unrevealed to us (May 1951).

In the pursuit or harvest of a marine mammal the biologist has a chance to watch his subjects in their native environment, to mark some for identification, and to collect specimens. At the home port or base he has further opportunity to examine specimens and to gather catch statistics by seasons, by sex, by territory, and so on. We emphasize the importance of obtaining specimens for the benefit of the biologist who may think of life history studies solely in terms of watching the subjects from a blind. Postmortem examinations are indispensable to an understanding of the number of young, the percentage of successful breeders, the age composition of the population, the age at sexual maturity, the sex ratio, the incidence of disease, and other desiderata too numerous to list.

Of equal importance, though harder to obtain, are life history facts derived from patient study of undisturbed marine mammals. The studies by Steller of the northern sea cow and fur seal in 1742 remain as classics of their kind (Stejneger 1936). Gunther (1949) comments favorably on the advantage of studying whales from a research vessel rather than a whale catcher. On a whale-marking voyage into the Antarctic he obtained data on respiration, swimming, diving, feeding, communication, and other behavior traits.

Lastly, certain facts with regard to the anatomy and behavior of marine mammals can only be obtained through observations of specimens held in captivity. The data so obtained are within the scope of the present assignment dealing with ecology, for they permit valid deductions as to the behavior of the species in the wild. For example, in the remarkable Marineland Aquarium of Florida, McBride and Hebb (1948) have established the fact of vocal communication among dolphins. And the present writer has gained information on the food requirements and the moulting of seals by observing captives in various American zoos (Scheffer and Slipp 1944; Scheffer 1950). Using ingenious devices, Irving, Scholander, Fetcher and others have studied the physiology of captive seals, dolphins, and manatees. As a result, the

responses of marine mammals to their saltwater environment are better understood.

Equipment. Certain devices and techniques useful in the study of marine mammals are already familiar to the dry-land zoologist, and others are familiar to the ichthyologist. We shall discuss first the tools needed in capturing and measuring marine mammals and describing their physical aspects.

On occasions when sea mammals cannot be obtained on land or ice they must be hunted by boat. The Japanese, highly successful in the commercial pursuit of seals and dolphins, use a power vessel 70 to 80 feet in length fitted with a pulpit at the bow (Austin and Wilke 1950). A smaller boat is uncomfortable on the high seas and a larger one cannot be turned quickly enough to salvage wounded animals.

For obtaining specimens, a 12-gauge shotgun with No. 00 buckshot works well on seals and dolphins; a Greener harpoon gun on dolphins and small whales (W. W. Greener, Ltd., 40 Pall Mall, London, S. W. 1). Staff members at the Marineland Aquarium have developed giant tongs of monel metal which, when thrown around the caudal peduncle of a playing dolphin, seize the animal and enable its capture alive. La Terza (1941) describes a hypodermic harpoon for narcotizing sharks, while Phillips (1948) describes a conventional harpoon used in the basking shark industry. Unless at very close range, a .30 caliber rifle is needed to kill seals weighing more than a ton. Harbor seals may be netted at the mouths of small sloughs or estuaries on a falling tide (and sea otters likewise, according to old reports). Dolphins and small whales are occasionally taken by accident in gill nets, tangle nets, or fish traps, but more often are stranded by falling tides. The killer whales, *Grampus* and *Pseudorca,* seem to be helpless inshore on an ebbing tide, for there are repeated instances of groups of them stranding.

Tools for measuring and weighing should be of corrosion-proof metal if possible; stainless steel, monel, chrome, or nickel (Glogau and Co., 538 S. Clark St., Chicago, Ill.; Gilliland Instrument Co., 3124 E. 14th St., Oakland, California). Convenient tools are calipers reading to the nearest millimeter, 15 centimeter rule, meter stick, 2-meter steel tape (or longer), beam steelyards (scales) of 200 and 1200 pound capacity (John Chatillon and Sons, 93 Cliff St., New York), inexpensive brass spring-scales or balances as required, block and tackle with three-fold purchase for hoisting specimens.

Dolphins are best photographed while suspended by the tail on this tackle; seals while lying on the deck. To avoid light reflections, wet, shiny animals should be photographed out of full sun. At sea it is often necessary to carry the specimen between decks out of the weather and to photograph it by flashlamp. For weighing seals on land, three 12-foot spruce or stout bamboo poles can be carried and fashioned into a tripod to support the scales (Doutt 1940). Quiring (1943) weighed whales on land, piece by piece. Ideally, specimens taken at sea or on offshore islands are photographed in the natural state and then frozen hard for careful study later in the laboratory.

Lacking refrigeration facilities, tissues can be preserved in 4 per cent formalin (commercial formalin 1 part: water 9 parts); pelts in three-quarters-ground salt, and skulls in rough dried condition. The enameled, 5-gallon, wide mouth berry tin used throughout the United States is a handy container. Two cans will fit neatly in a wooden oil case (capacity, two rectangular 5-gallon gasoline cans) and will hold formalin solution for at least two years at room temperature. A 2½-gallon glass jar with wide-mouth screw cap and bail is good for corrosive liquids such as Bouin's solution, although subject to breakage in transit. For long voyages and rough treatment, paraffined kegs and barrels are safest. Anatomical bits may be placed in cotton salt-bags or squares of cheesecloth, with a rag-paper label inside and out. For the freezer, there are many transparent polyethylene bags (freezer bags, turkey size) and waxed-paper cylinders now on the market.

Skulls of marine mammals are best cleaned by dermestid beetles, followed by a careful rinse (or boiling for adults) in 10 per cent aqueous ammonia. In an emergency, adult heads can be boiled in the field with ammonia, trisodium phosphate, or slaked lime, though at the risk of losing some of the teeth. Ammonia is preferable since it degreases the skull while softening the flesh. Few biologists have the ideal facility for finishing a marine mammal skull, namely, degreasing it by boiling in a reflux condenser with carbon tetrachloride. Seal and dolphin skulls hold an unusual amount of natural oil which, if not removed, eventually leaves a brown, discolored specimen.

Various marking devices have been perfected for facilitating the study of seal and whale movements and for identifying individuals in a population under scrutiny. For whales, a numbered stainless-steel tube about ten inches long is fired from a gun into the blubber, and recovered when the animal is killed (Hardy 1940). For fur seals and sea-lions, a standard cattle ear-tag is clamped over one digit of the hind flipper. For phocid seals, a button is wired through the fleshy base of the tail. Stainless steel, silver, and certain aluminum alloys have been successfully used in fashioning seal tags. We have had mixed success with monel. Hot-iron branding and, for temporary use, painting, have also been tried on seals (Rand 1950; Scheffer 1950c).

Biologists on the Pribilof Islands are finding that brightly colored vinylite strips fastened to a metal tag or to a fish hook are distinctive, short-term markers on fur seals.

Reconnaissance flights by airplane, dirigible, and helicopter have provided information on the distribution, numbers and, to a certain extent, the age composition of marine mammal populations. (Pinnipeds: Bartlett 1929; California Division of Fish and Game 1947; Canadian Department of Fisheries 1950, 1951; Dorofeev and Freimann 1928; Scheffer 1950b. Cetaceans: Grierson 1948.) Most aerial photos, however, do not show essential details. Progress seems to lie in the direction of special equipment; for example, the continuous strip camera which stops motion at high ground speeds and low elevations (Chicago Aerial Survey Co., 332 S. Michigan, Chicago, Ill.; Anonymous 1951). Here, though, maneuverability is sacrificed to high speed travel, and tests may show that the strip camera is impractical as a tool for marine mammal census work.

For seals and sea otters,—marine mammals that occasionally haul out on shore—patient study from a blind is indispensable. This requires the use of binoculars and a good weather-resistant camera. The Hasselblad, a portable camera recently placed on the market, combines many desirable features in a compact, 2¼ by 2¼ inch, quick-into-action camera, although it is expensive. (Willoughby's, 110 W. 32d St., New York.) (This is the writer's opinion based on land and sea experience with both smaller and larger cameras.) On a northern fur seal rookery we recently took photographs of a group of families at five day intervals between May and September. Comparison of the results enabled us to fix rather closely the time schedules of the various seals in attendance during the summer. For example, the adult males were all on land by 30 June; the height of the pupping season was 13 July; the nursing females began to desert in the second week of August; and so on.

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THE USE OF TAXONOMY IN ECOLOGY

In a recent article, Fosberg (1950) pointed out the desirability of documenting ecological researches by filing specimen vouchers of the plants studied. The present author is in wholehearted agreement with this suggestion, but feels that what is required is not only the mere documentation of itself, but rather the additional realization on the part of the workers of what constitutes adequate documentation. The need for adequate documentation is immediately apparent to the worker who is familiar with modern plant taxonomy, even at the elementary level, yet as Fosberg has mentioned, the majority of recent ecological papers are undocumented by specimens. The obvious conclusion is rather startling.

To some workers, unfortunately, the word "taxonomy" is synonymous with plant identification. According to such people, a competent taxonomist is one who can identify plants, and thus, facility in plant identification is a sign of competence in taxonomy. Reference to any standard dictionary will dispel such a concept. The derivation of the word "taxonomy" implies a grasp of the fundamentals of classification, not the techniques of identification. "Classification" implies sorting into groups or classes, either physically or mentally. Hence one may identify each plant of a group of specimens, through the use of keys, or through familiarity with the material. On the other hand, one may classify a number of specimens by sorting them into groups, using any criteria that he may choose. One cannot, however, classify an individual plant.

Since taxonomy is concerned with the principles of classification, it deals with the principles involved in sorting a mass of heterogeneous specimens into groups. The principles of taxonomy have not always been constant; they have changed as the objectives of taxonomy have altered through the years. Prior to the advent of the theory of evolution, one of the major objectives of taxonomy was to facilitate the identification of those species which had been originally created. Later came the natural systematists, whose major objective was to place each species next to those which it most closely resembled. At the present time, with the general acceptance of evolution, the major objective is to determine plant interrelationships, in an attempt to develop a phylogenetic system, in which each plant will stand next to those to which it is most closely related. The plant groups with which the taxonomist deals are usually named for future reference, hence the close relationship between taxonomy and nomenclature. The assigning of a name to a particular specimen by identifying that specimen with a previously named group of plants is merely "plant identification," which unfortunately still masquerades occasionally as taxonomy.

Probably every ecologist would agree that plant identification is important in his work. How else can he inform other workers of his materials, except by using plant names? What is the source of the names which are applied, and is the source infallible? If the worker uses keys, manuals, floras, and other similar means of identification, the names may or may not be correct. After all, the authors of these works were human, and subject to human fallibility. They were faced with large amounts of material, and a limited amount of time, so they applied their knowledge of the principles of plant classification to the best of their ability. However, they usually had neither the time nor the material to concern themselves with any but the most obvious infraspecific entities. Thus, in the majority of "floras," the various species appear to be placed in neat compartments, separated by rigid key characters. Students working in plant identification commonly think of a plant genus as being divided into a series of quite discrete species, and are quite worried when a specimen does not fit the key. Such worrying is indicative of a concept of a static species, where uniformity is expected. Unfortunately, such uniformity rarely exists in nature.

It has long been known that specimens referable to the same species show variation in their morphology. This variation is often coupled with variation in habitat, so that it may be said that plants of the same species from different environments often show a difference in morphology. There are two explanations of this phenomenon. One of these is based upon a concept of homogeneity of the individuals which comprise the species, and is unfortunately held by the majority of persons who have been exposed to work in plant identification without work in taxonomy. This is the view of Bonnier (1890, 1895) and of Clements (1929), and of some contemporary workers, who held that the variation of morphology observed in nature was the exclusive effect of the environment upon the individual plant. They also held that the transplanting of an individual from one habitat to another would result in changing the morphology of the transplanted individual to that of the locally-growing members of the same species, or even to that of local members of different species of the same genus. A moment's reflection will show that such a view is based upon a concept of species in which all members are genetically uniform; that all members of the same species have the same wide range of tolerance for each of the physiological factors, and the same wide range of morphological expression. It is interesting to re-

mark that the experiments which are cited to support this point of view were not adequately documented with herbarium specimens; nor did the workers invariably preclude the possibility of the invasion of the transplant sites by local plants; neither did they succeed in changing one "species" into another unless there was already a related species in the new environment.

The other explanation of infraspecific variability is that offered by Kerner (1895), Turesson (1922), and by Clausen, Keck, and Hiesey (1940). These investigators agree that the species is not a genetically homogeneous unit, but that throughout the range of the species there are numerous small populations, each with its own limited genetic constitution and with its own ranges of tolerance for the various edaphic and climatic factors, and each with its own range of morphological expression. In other words, the genetic constitution of the plant, which controls the tolerances of the individual, determines whether or not this individual can grow in any definite locality at any particular time. The morphological appearance is governed by the effects of those genes which are linked to those affecting the physiology. In contrast to the work of Bonnier and Clements, the studies of Turesson and of Clausen, Keck, and Hiesey are meticulously documented with herbarium specimens which show the inherent constancy of the above-mentioned populations under controlled transplant experiments.

Normally, transplanting an individual will produce changes in the physiology and morphology of the individual, within certain limits. What these limits will be can be determined only by experiments. In 1922 (b), Turesson reported on transplant experiments with two species of Lysimachia. Both of these species had forms which grew in either the sun or shade. In each case, the shade form had larger, thinner leaves with longer internodes. Transplanting of *Lysimachia vulgaris* from sun to shade, and vice versa, showed that the difference in morphology was due to the environment alone, whereas transplanting of *L. nummularia* showed that in these populations the difference between the sun and shade forms was genetically fixed, since the original morphology was retained after transplanting.

Recent investigations have demonstrated the existence of genetically diverse populations in practically every species studied. Even in apomictic species, mutations occur and accumulate in the several apomictic lines, so that these species are also genetically heterogeneous. Such genetic dissimilarity is increased through occasional outcrossing. In view of such demonstrated infraspecific diversity, any concept of the "tolerance of a species" is apt to be misleading. One may speak in terms of the tolerance of a growing specimen for certain factors, or one may speak in terms of the physiological limits of the most extreme biotypes of the species with respect to certain factors. In the latter case, no one plant will possess the ranges of tolerance ascribed to the species. Since biotypes of the same species do not necessarily possess the same physiological tolerances, or the same morphology, the occurrence of the same *species* in different habitats gives no definite clue as to the recurrence of the same environmental conditions. This is particularly true in the case of wide-ranging species, which normally contain a large number of biotypes.

In the recent past, the effects of the environment upon the plant have been determined by comparisons of the growth of two members of the same species from different habitats. Let us consider the validity of such conclusions. Following this procedure to a ridiculous extreme, the effect of the environment upon "red cedar" is extremely striking, as shown in the table below:

	Locality	
	Northeast Coast	Northwest Coast
Height	Up to 30 m.	Up to 60 m.
Reproduction	Dioecious	Monoecious
Cone scales	Fleshy, Coalescent	Woody, Free
Seeds	Wingless	Winged

The above table is not a valid means of showing the effect of the environment upon the plants since the plants used are not equivalent. The "red cedar" of the northwest coast is *Thuja plicata* Donn, whereas the east coast tree is *Juniperus virginiana* L. The above attempt to equate these two plants appears ridiculous, but the reason that they cannot be considered equivalent is simply that they are different genetically. They are placed in different genera because of the dissimilarity of their genetic constitutions, which is reflected in their dissimilarity in both morphology and physiology. However, is it any more reasonable to attempt such equation with plants, despite the fact that they are referable to the same species, where the genetic constitutions of the plants are also dissimilar?

The methods of recognition and delimitation of the infraspecific entities, together with the assignment of nomenclatural category to such entities, form an integral part of taxonomy. This particular phase of taxonomy is of primary importance to practising ecologists. While, as Fosberg has pointed out, the documentation of experimental work with herbarium specimens of the biotypes used will help to alleviate the present situation, this is really a mechanical operation which could result in additional confusion if the documentation were not taxonomically sound. Thus, it would be highly desirable, if not mandatory, that students of ecology be

thoroughly familiar with the content and scope of modern plant taxonomy. This implies considerably more than a grasp of the techniques of plant identification.

Since the majority of the genera with which the ecologist deals have not been worked over to the degree required in ecology, it should mean that the student be competent to deal with the fundamental taxonomic concepts within the groups of plants with which he is working. He would then be very definitely aware of the limitations of the validity of his conclusions in cases where the taxonomy was weak. It is immediately apparent that greater insight into taxonomy would require further work on the part of the student. Strange though it sounds, it has been suggested to the author that students are too busy in ecology to acquire an adequate background in taxonomy before embarking upon research. The conclusions of such students are frequently based upon erroneous taxonomic data. The question then arises, if the data are incorrect, how can the conclusions be valid? A competent student can never be too busy to acquire the tools necessary to do good work. Hence this plea for sound taxonomic practices in ecological research, including the recognition not only of the need for documentation by permanent specimens, but of *adequate* documentation. It would be safe to file herbarium vouchers of the actual plants studied. Certainly the vouchers should be of the identical biotypes used. The documentation process may vary with the species under consideration. The process could be different, for example when dealing with an apomictic species as contrasted with a cross-pollinated species. Seeds would be valid only in apomictic species, since the seedlings of other species are not normally identical with the plant bearing the seeds, even when this plant has been selfed. Living plants of the biotypes studied are advantageous, but are too space-consuming and evanescent. The major advantage of herbarium documentation is that one can say in effect, "This is the particular plant studied in this piece of work, call it what you will." Then, if the species is later subdivided into lower categories, the experimental work can still be tied in with the particular plant, and its new category.

Very obviously, such a program would increase the co-operation between the taxonomists and ecologists to their mutual advantage, for while the ecologist can benefit from the taxonomic data, the taxonomist can benefit to an equal degree from the ecological data.

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ECOLOGY AND THE SOCIAL SCIENCES: A REPLY

The recent note by Frederick E. Smith (*Ecology*, **32**: 763–764, 1951) is of interest since it postulates that ecology, strictly speaking, deals with phenomena which are genetically determined, thus excluding (unless by special dispensation) the environmental relations of man, which are culturally determined.

The heart of Smith's argument lies in the following quotation: "because culture is absent in most species, and negligible in all except man, a study of the environmental relations except those of man includes no sociology. And because genetically determined ecology in man is vestigial, a study of the environmental relations of man includes no ecology (except, of course, applied ecology . . .)." The key to this quotation, in turn, lies in the two words "negligible" and "vestigial."

Granting all difficulties, it is fair to question whether all students of the higher vertebrates would concede that the role of learned behavior (*i.e.*, culture) in organisms other than man is

negligible. Similarly, it is in order to ask whether, for example, physiologists and psychologists would generally admit that genetically determined ecology in man is vestigial.

Such inquiries, however, may be deferred until we answer a more central question. Is not the business of ecology the consideration of interrelationship between life and environment, taking that interrelationship as a phenomenon per se? Certainly the phenomenon exists, and since it does, are not those who make it their business concerned to study it in all of its aspects, whether the process in any particular case happens to be genetic, cultural, a mixture of both, or problematical?

In the terms—plant, animal, human, and general ecology—there would seem to be a sufficient range of simple symbolism for any ecologist to make clear what he is about.

We grant the need to keep in view the uniqueness of man. But this need not preclude an ecology of man, so long as this ecology is not prejudiced by assumptions concerning the nature of the relationships between man and an environment. Given their proper historic depth, such studies will reveal that, as in physics, for every action there is a reaction. For example, Beilmann and Brenner's recent study of the Ozarks demonstrates how changing cultural practices have altered the total ecology of that region: botanical, animal, pedological, economic and hydrologic.

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MEASURING DIAMETER CHANGES IN SMALL STEMS

The necessity for an efficient method of periodic measurement of the changes in stem diameter of several shrubs occasioned the development of the technique described below. The dendrometer devised by Daubenmire (1945) is not adapted to the measurement of growth in stems with diameters of 2 inches or less. However, the technique described is an adaptation of Daubenmire's method. The critical study of the method by Fowells (1941) is also pertinent.

In practice, one-fourth inch discs are stamped from 0.020 sheet aluminum and glued to op-

Fig. 1. Stem diameter changes can be determined by periodic measurement with a micrometer caliper of the distance between small aluminum discs attached permanently to the stem.

posite sides of the stem using acetone cement. This was the best of several types of glue used under field conditions. Growth in diameter is considered the increase over a time period in distance between these fixed plates as measured with a micrometer caliper having a friction stop (Fig. 1). These instruments are available at very little expense (less than $10.00 for the caliper measuring up to 1 inch) and register to 0.001 inch or 0.01 mm depending upon the preference of the investigator.

It is desirable to remove loose bark fragments prior to securing the discs to insure a firm base, but care should be taken that traumatic effects are not induced in the stem. The disc location may be obtained by holding the caliper lightly in position on the stem and marking the respective locations of the spindle and the anvil. Measurement variations are reduced considerably and the discs are more secure if they are positioned on the stem with the caliper until the adhesive begins to harden.

Perhaps the greatest disadvantage of this method is the number of calipers required if a considerable range in stem diameters is included. However, the simplicity of the installation and the ease of manipulation permits the measurement of a large number of stem diameters within a reasonable time and with sufficient accuracy for critcial analysis of the data obtained.

Acknowledgment

The writer acknowledges the helpful suggestions and field work of J. A. Tynan, Field Assistant, Texas Agricultural Experiment Station, Substation 19, Winter Haven, Texas, in the development of this procedure.

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WHY DO PLANTS WILT IN COLD WEATHER?[1]

Plant physiologists have maintained that plants wilt at freezing temperatures primarily because of injury to the cellular protoplasm (Kramer 1949). But the results of soil-moisture studies with Colman fiberglas soil-moisture units seem to indicate that ground freezing is at least as important as protoplasm injury in causing the death of plants.

The Colman soil-moisture unit (developed at the California Forest and Range Experiment Station) is a device that reflects soil-moisture conditions (Colman 1946). Each unit contains a strip of fiberglas cloth that quickly absorbs and releases moisture; it tends to be in equilibrium with its surroundings. When an electric current is sent through the fiberglas, it encounters a resistance inversely proportional to the amount of moisture held by the fibers. Thus, a unit placed in a soil containing very little moisture will offer a high resistance to the passage of an electric current; but a unit in a wet soil will offer little resistance. Soils at field capacity offer a resistance in the vicinity of 1,000 to 2,000 ohms. Soils at the wilting point offer a resistance of approximately 100,000 ohms.

When a soil is frozen, the fiberglas units react as though the soil had been desiccated. (In this study, the soil samples were frozen by being placed in the freezing compartment of an ordinary refrigerator.) The soil may be at field capacity, but as the soil is cooled, its resistance increases steadily to the freezing point of the soil solution; at that point the resistance increases to a resistance between 10^6 and 10^7 ohms. If the soil is drier, it simply reaches the maximum resistance in less time.

Figure 1 illustrates this. The curves are for the upper portion of the B horizon of a Hazleton stony loam soil (tentative nomenclature by U. S. Department of Agriculture) in Pennsylvania. Curve AB shows that as the moisture content of the soil decreases, its resistance increases; and that its wilting point (considered as 10^5 ohms) is at about 27 per cent of the dry weight of the soil. Curve BC indicates that the soil, when close to saturation, will freeze solidly in about 9 hours (with temperatures as obtained in the refrigerator used). Curve EF shows that the same soil, when its moisture content is reduced to 39 per cent (somewhat less than field capacity) will freeze solidly in about 6 hours. The curve GH is the 10^6 ohms line; it is the wilting-point line.

This figure illustrates the results from one specific soil sample. Other samples will vary only in the slope and relative position of the curves forming the surface ABCD. In all

[1] The writer thanks Mr. Harry Price, of the Northeastern Forest Experiment Station, for his help in conducting the freezing experiments.

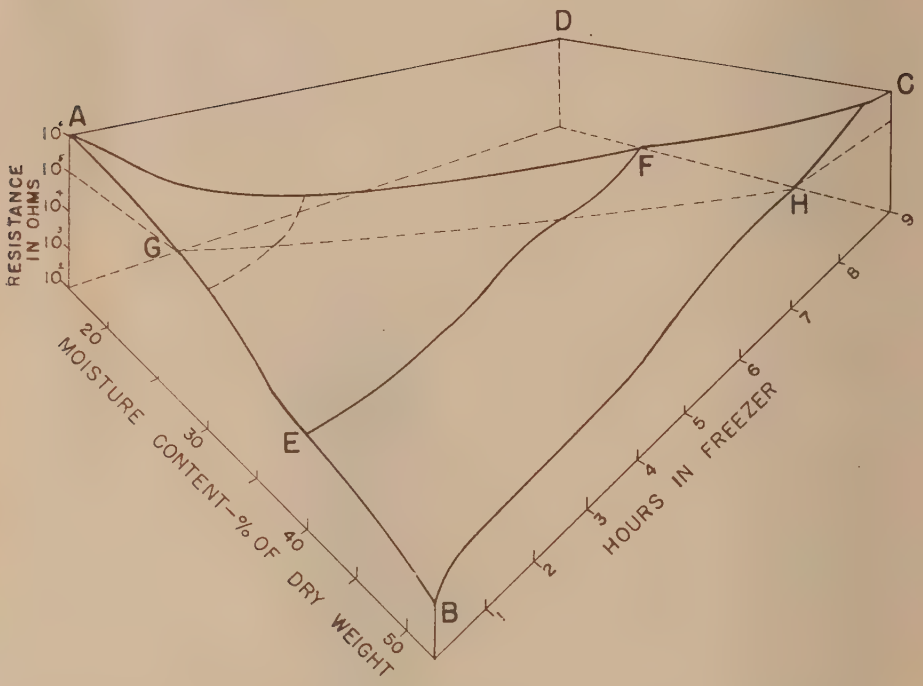

FIG. 1. The resistance offered by the soil solution at varying concentrations and temperatures. A dry soil and a frozen soil both offer very high resistances. A concretely frozen soil offers a resistance greater than the resistance obtained at the wilting point of the soil. The curve GH is the wilting-point line: 10^5 ohms resistance.

cases studied (42 soil samples of three different soil series) the resistance of the concretely frozen soil was well above the wilting-point resistance of the soil.

SIGNIFICANCE OF DATA

The data seem to indicate that a frozen soil is, physiologically, a dry soil. Concretely frozen soil is equivalent to a soil that is below its wilting point in moisture content. Hence, a plant growing in frozen soil has no moisture available for growth; and if it transpires, it will wilt.

However, in connection with soil freezing, there are a few other factors that must be considered: the depth of the frost line, the depth of the soil, the rooting habit of the plant, and the depth of the snow cover. Three examples will illustrate the relation of these factors. A plant whose roots are below the frost line will not wilt. The same plant will wilt if grown in a shallow soil whose depth is less than the frost line. But, if the snow cover is deep enough to cover the plant and thereby prevent transpiration while the soil is frozen, this plant will not wilt.

Field observations tend to corroborate these theoretical considerations. A colleague who was formerly a farmer informed the writer that, on his farm, winter wheat growing in small depressions in which the snow collected grew luxuriantly; but in the remainder of the field the wheat was poor. Although the snow that accumulated in the depressions was not deep enough to prevent ground freezing, it did prevent transpiration, thereby leaving the wheat in a healthy condition so that it grew well when the soil thawed.

APPLICATION OF RESULTS

From these observations it appears that the advisability of planting coniferous seedlings in the fall may be decided by comparing the height of the seedlings with the normal winter snow depth, and the depth of the seedlings' roots with the expected depth of frost. Fall planting should probably be avoided in regions that have severe

winters but little snow; on the other hand, it would probably be successful in areas that normally have a deep accumulation of snow.

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THE OCCURRENCE OF A TERRESTRIAL ISOPOD IN PLANKTON

On 25 July 1951 the writer, together with Charles Horvath and Howard Winter, made a surface plankton haul from Lido Island to the entrance of Newport Harbor, Orange County, California. The haul was of one hour and thirty minutes' duration (3:00—4:30 P.M.) and at all times the net was kept at the surface. The boat was directed down the center of the channel, being always forty feet or more from shore. The sample contained copepods, cirolanid isopods, planktonic algae, a few arrow worms, some blades of the eel grass *Zostera,* a few pieces of paper, some sand, and two specimens, a male and a female, of the terrestrial isopod *Tylos punctatus* Holmes & Gay (Van Name, 1936) each about 9.0 mm. in length and 4.0 mm. in width.

Tylos and its close relatives are halophil terrestrial isopods which inhabit sandy beaches under logs and debris at about the high tide line. The sand is usually dry and seldom inundated by the water of high tides. *Tylos* lacks the ability to swim. Typically it is found around bays and estuaries and it has never been reported from beaches along the open coast to my knowledge. This gives *Tylos* a markedly discontinuous distribution along the coast from bay to bay.

Speculation has at times arisen as to how this distribution has been brought about. A currently accepted hypothesis accounting for the distribution of organisms such as *Tylos* suggests that they were carried by ocean currents from one bay to the next. To my knowledge there exists no record of *Tylos* or of its related species having been taken in plankton before. For that matter this constitutes the first record of the species *T. punctatus* from Newport Bay. Previously it had been reported from San Diego and Laguna Beach, California. The specimens when collected were quite lively and apparently were suffering no ill effects from their submersion. Air pockets trapped around the bases of their appendages and pleopods appeared to assist in keeping them afloat. This record clearly accentuates the possibility that *Tylos* might obtain its interesting discontinuous distribution along the coast by being transported by surface currents either by clinging to floating objects or simply by floating by itself.

Summary

The terrestrial isopod crustacean *Tylos punctatus,* which lives on beaches but cannot swim, has been taken alive in surface plankton hauls at least forty feet from shore in Newport Harbor, California. Such an accidental occurrence may be common enough, or rare enough, to account for the discontinuous distribution of the species.

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REVIEWS

Deciduous Forests of Eastern North America [1]

The publication of Dr. E. Lucy Braun's book on "The deciduous forests of eastern North America" is timely and of no mean significance for future developments in the rational use of eastern American lands. In a sense this book parallels in significance for the eastern part of the continent the great work prepared in the 1870's by Sargent on the forests of North America. As that work did for its time, so the present description of the deciduous forests sets the stage for more intensive study, and eventually for a more intelligent use of the forests.

Scientific forestry in America has, from its inception in the late 19th century and the first years of the 20th, been most heavily concerned with coniferous forests. Its early experimental work was laid in the areas then thought of as the white pine and spruce regions of northeastern United States and adjacent Canada, and in the great coniferous forests of the Northwest. Its methodologies and most of its ideas were derived from the forestry of northern Europe. Most of the white pine and old-growth spruce of the Northeast have now been used, and in many parts of this region the regeneration of these forests to their former conifers has proved to be impossible with our present knowledge and within the present or foreseeable economic structure.

The results of this change are far-reaching both in industry and in the development of American forestry. Industries based upon the eastern coniferous forests are remaining in place by making major adjustments to changing supplies of timber, or are moving to other regions west and south, or are disappearing. Those that have moved to the Far West are still deriving their raw materials from virgin coniferous timber, or are harvesting second growth which there remains coniferous. Those that have moved to the southern coniferous forests are finding increasing difficulties with the regeneration of southern pine, though in some parts of the South the success of this venture appears to be feasible.

In the Northeast and the Lake States the persistence of wood-using industries has depended upon many factors; chief among these have been improved transportation and the remarkable development in recent years of wood technology and utilization. The cutting of pine and spruce in the Northeast has been followed by the development of hardwood forests over vast areas. The modern utilization of these hardwoods, particularly for the fiber and chemicals they contain, promises a continued and expanding base for wood-using industries. This has given rise to a rapidly enlarging interest in the silviculture and management of all our native eastern deciduous forests.

The practical management of our eastern forests is adrift in a stream of natural change over which there are as yet only pitifully small controls. Knowledge of such change was only in embryo when Sargent's report on North American forests was published. This knowledge had scarcely more than begun to take useful form during the early years of American scientific forestry. Although its implications are now known to most foresters and other plant scientists, its wide application has been impossible because of its limited scope and because of our hazy knowledge of the nature and geography of the forests themselves. It is against this background that the stature and timeliness of "The deciduous forests of eastern North America" becomes apparent.

Dr. Braun's book is in three parts. In the first, following a brief introduction, she sets forth the basic concepts in forest ecology to which she adheres throughout the book. These concepts, with their associated terminology, cover the units of vegetation with which she deals, and the ideas of forest development and habitat which she applies to her reasoning with regard to forest history and distribution. A general survey of the soils of eastern North America is included.

The largest section of the book, Part II, contains a description of the deciduous forests. It is based upon an immense amount of field observation made by Dr. Braun herself, supplemented by careful selections from the work of other students. In reality it is the consummation of Dr. Braun's life work. The bulk of her own field operations has been in the Cumberland mountain and plateau center of the hardwood region, but in recent years she has traveled widely throughout the entire deciduous forest. Although in most cases she has depended upon the studies of others for details concerning the forests of the outlying regions, she has made it a point to see them herself and to make comparisons based upon her own observations.

Part II contains the solid core of the book. In it Dr. Braun has not only described existing second-growth forests, but has carefully assembled all available data on the natural forest as it appeared to early settlers. These data are derived from historical accounts and from persisting remnants of pre-colonial forests. If she had ac-

[1] **Braun, E. Lucy.** 1950. Deciduous forests of eastern North America. xiv + 596 pp. Philadelphia: Blakiston. $10.

complished this alone, her work would have been of monumental value. It is altogether possible that her reconstruction of the natural forests for this vast region has been done, as it were, in the nick of time. In any case, the difficulty of doing it in the future, what with rapidly increasing use of the hardwoods, will increase so greatly as to preclude its possibility except at large expenditures of time and energy.

The significance of Dr. Braun's reconstruction of the primeval forests to the future development of hardwood silviculture can hardly be overestimated. The proper management of our complex hardwood forests is so poorly worked out that even the basic points of departure in silvics and forest geography are not understood. In lieu of detailed knowledge of the ecology of our forests, these points of departure must be in the natural productions of the land as they appeared in the precolonial forests. Dr. Braun has produced an outline for these "datum planes" upon which we can build.

Part II consists of ten chapters, the first of which is a general review of the structure of the deciduous forest as a whole. The remaining nine chapters describe its subdivisions (regions) as Dr. Braun has defined them. They are as follows: mixed mesophytic, western mesophytic, oak-hickory, oak-chestnut, oak-pine, southeastern evergreen, beech-maple, maple-basswood, and hemlock - white pine - northern hardwood.

Throughout her organization of regions Dr. Braun has been much influenced by the general relationship between forests and topography. Most of the defined forest regions are related not only to existing topography, but to the physiographic development by which the existing topography has come into being.

It will be noted that the first division described is the mixed mesophytic. It is probable that Dr. Braun's prime contribution to our knowledge of the deciduous forest as a whole is her interpretation of the significance of the mixed mesophytic forest as the basic center for the evolution and distribution of all the other divisions.

Part III is entitled "The evolution of the present pattern of forest distribution." It consists of six chapters dealing with general problems, paleobotanical sources, disjunct occurrence of species and communities, a brief statement of the physiographic history of the region, an attempted chronological reconstruction of forest history, and a study of the interrelations of the forests within the whole complex.

The deciduous forest in all its modern complexity is considered to have been derived from forests of the same nature which presumably were widespread between the Rocky Mountains and the Atlantic Coast in mid-Tertiary time. Dr. Braun summarizes the fossil evidence for the existence of this forest and of its progenitors in the Cretaceous. She conceives it to have been relatively uniformly mixed mesophytic, but with a certain amount of latitudinal differentiation. She believes that the aridity which developed in the interior of the continent during the Tertiary eliminated the Great Plains elements of this forest. Physiographic changes in the East, occurring in the same period and perhaps accentuated in their effects by western aridity, were sufficient to bring about the basic segregation that still exists in the present deciduous forest region.

Miss Braun considers, therefore, that the segregates in which the oaks became dominant (oak-hickory, oak-pine, oak-chestnut, and the white oak type) had already been formed at the close of the Tertiary, and were established in their present regions. The nature of late Tertiary segregates in the region north of the glacial boundary is, of course, unknown. However, she proposes that the hemlock - white pine - northern hardwood segregate existed before the Pleistocene in the Northeast, and that it probably persisted throughout the Pleistocene in the northern Allegheny Mountains and the Allegheny Plateau. The exposure of new lands at the retreat of the Pleistocene ice sheets led to the expansion not only of the hemlock - white pine - northern hardwood type, but also to the development of the beech-maple and maple-basswood segregates.

Dr. Braun marshalls a great deal of evidence to indicate that the advance of the Pleistocene ice brought about relatively unimportant changes in the forest geography of the region south of the ice. She proposes that there may have been a certain amount of altitudinal displacement on the mountains, and some infiltration of northern species. However, she does not believe that these greatly influenced the composition of the more southern forests.

The book closes with an extensive bibliography (538 titles), an index to common and scientific names, and a general subject index. The whole book is profusely illustrated with well-selected half-tone photographs, carefully chosen tabular data on the content of forest communities, and useful maps. A general map of all the forest regions is inserted at the back.

Modern ecological plant geography, particularly as it has grown in America, has been concerned primarily not so much with the simple geography of vegetation as with the development of vegetation. This emphasis upon vegetational change is to be seen in the very fabric of the science. Although some of its roots are to be found in European work of the late 19th century, it has had its largest development in America during the past 50 years. Its primary design first appeared in the work of Cowles in the region around the southern end of Lake Michigan. It was based in large measure upon

an area of correlation elaborated by Cowles and his students—a correlation between the development of vegetation and the development of land forms. A primary impetus for it seems to have come from the contemporary studies of the cycle of erosion by the physiographer, William Morris Davis.

Ideas developed in the Chicago school were quickly picked up by many students in the Middle West and the Great Plains region. The most articulate of these students was Frederick E. Clements who developed the idea of plant succession to such an extent that it has become the organizational base for most American ecological plant geography.

Particular emphasis upon the development of vegetation has led inevitably into a maze of problems, the statements of which have become burdened with an impenetrable tangle of facts and assumptions. Once completely imbued with the idea of development, one has a strong tendency when looking at a stand of vegetation to see it not for what it is, but for what it has been, or for what it is becoming. Dr. Clements once said to this reviewer, while commenting upon the work of a contemporary ecologist, that this individual seemed to be able to see only what was on the ground in front of him. This was meant to be a disparaging remark.

When existing reality thus becomes so transitory, the way is open for endless theorizing on what may happen in the course of development. The plant ecologist attempts to bring order out of this chaos with the concept of "climax." It is assumed that all vegetation is developing toward some kind of more or less stable equilibrium, or has already arrived there. This does not solve the problems, because it becomes necessary to define climaxes.

Decision on what constitutes a climax rests upon our capacity to understand the relationship between a forest and its habitat, and to project this relationship over time. It is safe to say that with our present knowledge we are unable to state the relationship by processes of analysis and synthesis. Our knowledge of the genetics and ecology of the individual species of trees is so slender, and our inability to measure and synthesize the multitude of external environmental factors is so marked, that the method of analysis and synthesis seems for the time being impracticable. Even if we were able to draw up such relationships for individual species, we would still be far from our goal because of the complex nature of most communities.

The element of time introduces still further difficulties, particularly in the study of forests, for it becomes necessary to project our imperfect knowledge of the interactions of trees and their habitats over comparatively long periods of time in order fully to define climaxes.

In the absence of tangible results from analysis and synthesis, therefore, we look for indications of climaxes in what we can reconstruct of the precolonial forest, or in whatever trends of development we can detect in existing second-growth stands. To make these methods workable, however, we have to assume a certain amount of stability in general forest-habitat relationships. It is common practice to proceed with cases of forest succession as though the climate were a relatively stable influence within which changes occur at such a slow rate that they are almost imperceptible. The same is commonly thought to be true of most physiographic processes which affect land forms and soils. Out of these areas of relative stability come our concepts of climatic and physiographic climaxes. Climatic and physiographic changes do occur, however, some of them gradual and others cataclysmic. Correct definitions of climax by these methods therefore rest upon the assumptions that we know the rates and effects of gradual changes; and if the changes are cataclysmic, that we know what they are and can place them in time sequences.

In spite of the fact that Dr. Braun carefully defines her terms and concepts at the beginning of the book, some readers will have difficulty with Part II. Throughout her description of existing and precolonial forests, she has inserted the concept of the climax, and has attempted to place all existing forests in a climax or in some developmental sequence leading to one. She describes her forest regions in terms of forest climaxes, and in so doing she has raised all the problems that surround the definition of climaxes. For those who have found it difficult to utilize the theory of climax, her insistence upon it may be a source of distraction when they read her superb descriptions of the forests. It might have been better had she reduced her discussion of the deciduous forest regions to simple geographic descriptions, and placed her interpretations of succession and climax in an additional chapter of Part III.

These questions are, however, matters of opinion. They will give rise to an abundance of stimulating argument, discussion, and further research, which is as it should be.

Dr. Braun's basic philosophy of plant geography is derived in large measure from the ideas of vegetational history and development outlined by Cowles. Nevertheless she has manifested a large amount of divergence. Her training and experience in geology and physiography appear to have been far more extensive than is the case for most contemporary plant ecologists and plant geographers. While Clements and others were enlarging the theory of purely biological succession, she was more preoccupied with the history of vegetation as related to the development of land forms. Of equal or greater significance for the production

of the present volume has been her divergence into the field of floristic geography. Here she has fallen heir to a vast amount of information and suggestion that has scarcely been touched by most ecologists. Not only has she used this material effectively, but she has made notable additions to it in her own right. Further, not content with existing data on the distribution of species, she has seen and utilized the contributions now being made by modern genetics to the geography of plants. With these divergences she has made an immense contribution, not merely to the methodology, but to the breadth and depth of the philosophy of geographic botany.

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Ecology and History of the Bison [1]

This is one of those great books which will adorn the culture of a continent. It is primarily an historian's work and not a biologist's, but it illustrates perfectly the axiom that the ecologist cannot neglect history, and its fine critical quality should impress the ecologist with the need for as careful work in his historical studies as in his ecological observations. The naturalists, such as Hornaday, who have become our authorities on the buffalo, do not emerge with much credit from Dr. Roe's searching criticism. He places J. A. Allen's work, 1876, as much the best. Hornaday, following Allen, was the second professional scientist to study the buffalo in its wild state with definite purpose, but he was too late; he went onto the plains when the animal was almost extinct, and he had to depend so much on hearsay. Unfortunately, the rugged types who were supposed to know the buffalo so well and who could talk but not write, were not very reliable witnesses. They saw the animal from their own point of view only and could not orientate. Some of these men grossly exaggerated and told tall stories and one surmises that some of them were not so rugged on the range as they were in the smoking room. The Indians, as Dr. Roe points out, were excellent observers of the particular and were dependable in recounting the particular, but they were bad generalizers. It was a process of thought foreign to them but one to which the white man is much given, and one can imagine that the pressure of questioning would embarrass the Indian and confuse him into giving poor generalizations as a means of escape. Questioning between unlikes is not a good way of getting information anyway. The reader of this book, however, cannot help getting exasperated with those literate observers of the buffalo from the 16th century onwards, who committed themselves to writing, but who observed so badly. Dr. Roe gives the accounts of these men in their own words as far as possible and it is difficult to get precise information from them—"vast hordes," "thousands," "passing for several hours," and so often there is the tidy, or more probably the lazy, mind generalizing from particular incidents. Roe is more patient and states that his "central thesis in everything relating to buffalo is the high importance and (inherently) equal value of precisely such discrepant evidence."

There are unfortunately no maps in this book to supplement the author's painstaking chapters on the historical habitat, in which chapters he cites references from the earliest historical period onwards. It would seem that the spread of the buffalo over the plains and to the limits of its range was a relatively late phenomenon and was still in process when the white man came to America. Differing environments produced variant forms of the species and variant typical behaviour, which fact Roe goes to great length to establish. He doubts the common assumption of the plains as "the home" of the buffalo, but there can be no doubt that once the animal found them, they were a habitat much to its liking. The increase of the buffalo in the plains must have been phenomenal and its influence on the human population immense. We know that many tribes of Indians left the forests and the life of mixed hunting and primitive agriculture and became completely dependent on the buffalo.

It is Roe's principal thesis that the buffalo of the plains was not a regular migrant, but an irregular one, even to the point of being nomadic. He is therefore a severe critic of the theory of buffalo roads in constant use. This irregularity of movement of the buffalo herds caused the plains tribes of Indians to be nomadic also, to such an extent that their tribal boundaries were not sharp. Within these large, loose territories the Indians themselves were not always in contact with the buffalo. Movement of the animals was irregular enough for the Indians to go hungry from time to time. Evidence also appears in this book that white settlers in the early 19th century had frequent lean spells when the buffalo could not be found,

[1] **Roe, Frank Gilbert.** 1951. The North American Buffalo: a critical study of the species in its wild state. Toronto: Univ. Toronto Press. $ 12.

though they might be only thirty miles away or might turn up any time, quite suddenly.

Ecologists have often conjectured to what extent the buffalo advanced the regions of prairie. Roe thinks their actual effects in deforestation to be small, though by grazing they would prevent regeneration and the forest would die on its feet. The Indians, however, manipulated fire with a good deal of understanding, and certainly extended the areas of prairie—and consequently of the buffalo itself. For example, there are wooded hills in south-west Wisconsin which were prairie a hundred years ago when the Indians possessed them. A recent paper by Sauer [2] emphasizes that the prairie was a biotic climax, not a climatic one, and there can be little doubt that the *conjunction* of buffalo and Indian in the culture found on the plains was the formidable factor. The culture was symbiotic.

We may truly regret the absence of a few good ecologists for the period of the decline of the buffalo, the last of which east of the Mississippi was shot in 1820, and the herds west of the River were finished by 1886. We know that some traditional buffalo grounds such as wallows and licks became specialized in their herbage complexes, *e.g.,* the dominance of buffalo grass, and it would seem from the evidence accumulated in this book that there was often serious overgrazing as the vast herds moved about. These aggregations are themselves phenomena for which there is as yet no really good explanation, but their influence on the sward was searing. Colonel Dodge provides the one highly important figure for the density of these immense aggregations; he described the one through which he passed as being of the order of 15–20 beasts to the acre. This is a long way from being a solid mass, so often described but unbelievable except in episodes of stress, yet to a man in a prairie schooner looking over a plain, this density would certainly render the landscape "black" with the animals.

[2] **Sauer, C. O.** 1950. Grassland, climax, fire and man. J. Range Management, 3: 16–21.

There is no point here in recounting the terrible events of those last years of greed and slaughter. Roe pulls the figures to pieces, and shows how the anti-Indian bias had a good deal to do with the final destruction. It was deemed necessary to exterminate the buffalo if the Indians were to be subdued. General Grant for one refused to promote any legislation for protection of the animal. If that was indeed the policy, it was a terrible success, with tragic (and terrible) results still with us today. The plains Indians had over-specialized their culture on the buffalo as a continuing resource, which it doubtless would have been but for the eruption of European man and the growth of markets eastwards. The buffalo tribes made themselves hostages to fortune by their specialization and loss of variability of behaviour, and it is in these tribes that the greatest breakdown in Indian life has occurred.

The story of the buffalo is epic on the grandest scale and the imagination is fired if the spirit is grieved. The Briton honoured here by the invitation to review this book cannot resist wondering what consequences the buffalo and the plains Indians had for his country. These two in conjunction created a vast expanse of prairie ripe for the *rapid* conquest of the plough which let loose a flood of wheat. The consequences of that flood are now the congested populations of human beings which are treading out their very habitat and nibbling the roots of their subsistence, like rabbits in a warren.

Roe's book is not easy going and even his concluding summary fails as such. One must read it all, nearly 1000 pages, and some of it is tiresome. The numerous appendices are on varied subjects but are all pertinent and must be read. The reviewer, however, does not wish to quibble in the face of such service as Dr. Roe has rendered in compiling a vast source book, and by interpreting his data so scrupulously.

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America's Red Deer [1]

This Holarctic animal is a good example for the point of view that behaviour should come into our reckoning in taxonomy. The elk or wapiti of North America, the Altai deer or wapiti of Siberia, the diminutive red deer (comparatively) of Scotland—all behave similarly in a thousand facets of their lives, and if the opportunity arises, they interbreed successfully. Red deer-Altai-elk constitute a circumpolar cline with sufficient temporal and physical discontinuity to persuade us to give specific rank to each group. The elk of North America is the largest species in the cline and a magnificent member of the fauna of the continent. To one accustomed to Highland red deer it must always remain as fabulous as the elephant confronting the Cockney who exclaimed, "There ain't no such animal!"

It is fitting that Dr. Murie should write this

[1] **Murie, Olaus J.** 1951. The elk in North America. New York: Stackpole, and the Wildlife Management Institute. $6.50.

book for he spent several years making a study of the elk in its stronghold of the Yellowstone area of Wyoming, and he knows the animal wherever it is found in North America. Its former range there is interesting, assuming that it entered by the same route as the Indians, by the Siberia-Alaska bridge. It spread south and east but apparently did not go south of the 30th parallel of north latitude. The northern range receded and in historic times did not extend beyond 60° N, and that only in the route of its ingress, in British Columbia and Alberta, from the north-eastern corner of which latter Province the northern edge of distribution falls away steeply to the southern coasts of the Great Lakes. Although the elk was present north of Lake Ontario and in the region of Montreal, it did not go north into the Hudson Bay basin and Labrador. The elk is not the deer of the tundra or the taiga. The Atlantic may have been touched between New York and Washington, but again, the low, coastal, forested plain is not its habitat, though it may have entered them in winter. The elk likes mountains at its back, the temperate and—the word is used advisedly—delicious mountains which are set in North America's dry plains and basins. Those plains were wintering grounds.

Dr. Murie rightly dwells on the migratory habit of this animal. Seasonal movement is part and parcel of its life, and to the reviewer who would wish to include the red deer as the elk's little brother, the outstanding characteristic of the kind is mobility. This mobility allows elk and red deer to fill a definite ecological niche and to occupy a diversity of habitat; and with mobility is linked the other characteristic of plasticity of size. The great elk of the western states and the little red stag of the bare hills of the Hebridean island of Harris have been able to slide one way or the other on the size scale in a way few other beasts have been able to do and keep within a very characteristic shape and behaviour pattern. The elk, doubtless, would find it difficult to reduce size in a generation, but the red deer can expand almost like a trout. One day, in Tarbert, Harris, in the Outer Hebrides, the reviewer was looking at a magnificent series of antlers, obviously from one stag, and he was asked what their origin might be. The shape was far too beautiful for the great English or German deer but, of course, they were much too large for any Highland stag, let alone the extremely pretty but diminutive stags of Harris. His guess was a New Zealand stag of Scottish ancestry, for the species has there greatly increased in size. The truth was that it was a Harris stag picked up as a day-old calf in Harris, fed on the bottle and taken to Hyde Park, London, where it fed on good grass and portions of Londoners' *al fresco* lunches. The antlers were picked up each year and returned to Harris.

We may wonder how the elk came to its immense size, even beyond that of its Altai ancestor, and it may be suggested that in addition to the large amount of good limestone country, the ease of protracted orderly migration had something to do with it, given an organism so plastic in size. The reviewer noticed last year in California that the stationary black-tailed deer of the basaltic hills around Clear Lake were unduly small, and that the deer of the much poorer granite pavements of the Sierra were large and better-headed. These latter deer are strongly migratory. Altitudinal range greatly shortens the length of migration, but we should not let it mask the essential fact. The migrations of deer are remarkably orderly and persistent if we consider them community by community and not as a species over a large area. Thus, the elk of the northern Yellowstone country appear to descend north-westwards to winter range; Murie says that others come west through Two-Ocean Pass into the wintering grounds of Jackson Hole; others move southward towards Pinedale and the sagebrush plains.

The great value of Dr. Murie's book is in the immense amount of factual matter which he has gathered together and set down. The greater proportion of the data are from his own experience and investigations—and the result of this constant personal intimacy is a freshness in reading. One gets the impression, nevertheless, that the aim of the book is primarily to convey this factual information rather than to discuss it in relation to ideas and principles of modern ecology. The reviewer's only considerable adverse criticism is that the book is not quite up-to-date in the field of wildlife population dynamics and ecological theory. Reference to the bibliography shows omission of papers of the last 10–15 years which would have illuminated some chapters in the book. The imprint of the Wildlife Management Institute possibly called for the more practical treatment. The ecologist may have to hunt his material in this book, but he will have a pleasant time doing so.

Aspects of the life of the elk are pursued logically, chapter by chapter, *e.g.*, reproduction, natural enemies, parasites, disease, food habits; and the book concludes with chapters on elk population and elk management. Always, the reader will get his facts; if the author discusses the coyote as a natural enemy, then there is a table of analyses of a good number of coyote scats or stomachs. The food plants are named separately and in great variety, and are discussed as elk food. There are also excellent passages on food range as a whole, indicating the constant watch which must be kept on range

condition as the real pointer to stocking capacity. Range may still go on producing a large number of elk in good condition long after it is irreparably damaged. That is where the ecologist must point the truth and not be misled as the sportsman often is, in thinking that a very large stock can be maintained.

The present reviewer may be forgiven for constantly comparing phenomena in the life of the elk and of the Scottish red deer, for there is some stimulation to be got. Murie finds that among adult elk there are many more females than males. His figures are similar to those found by the reviewer for red deer in the Highlands. Murie cautiously finds the female elk to have a longer life span than the male, a fact definitely noticeable in red deer. And further, the fertility rate and the survival rate to one year are similar. Specificity would seem to be exceptionally strong, for the terrains of American elk and Highland red deer have now so many differences. We could reasonably surmise, for example, that the wonderful feeding conditions which have acted on the plastic character of cervine size have not affected fertility rates and population dynamics.

Production of the book is good but not very good. The reviewer's copy is rather unevenly inked and the halftone blocks need better paper and finer screens. The text is embellished by many of the author's beautiful black-and-white sketches.

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The Background of Plant Ecology [1]

We are greatly indebted to Professor Conard for this excellent translation of one of the classics of plant ecology. The better-known works of later European writers, especially Warming and Schimper, have cast a good deal of shade on these earlier descriptions of plant communities. But there are many surprises for the modern reader in this book. The sound rendered by contemporary scientific prose contrasts so sharply with the style of Kerner that we wonder seriously if these leisurely and flowery descriptions can really have been the point of departure of new developments in Ecology. Can the author have taken himself seriously enough to be the founder of a new science, the originator of a new direction?

Both the preface by Theodor Just and Conard's foreword situate Kerner's contribution at the origin of what was later to be called plant ecology. Its availability to the English-reading public (which is often exclusively English-reading on this side of the Atlantic) is most timely indeed. This book shows ecological thinking when it had not been freed from taxonomy as it was to be in the work of Raunkiaer; when autecology and synecology were not yet distinct, as Warming and Schimper were to make them. It shows the original continuity from a synthetic, natural-history point of view towards an analytic and even experimental approach.

Such a book also serves to remind us of the fact that ecology, in some of its phases, has now become a specialty and that it is now possible to operate within this narrowed discipline with an extremely restricted knowledge of either taxonomy and plant geography on the one hand or genetics and physiology on the other hand, not to mention geology and pedology. Kerner, as this and his other, better-known "Natural history of plants" testify, was a thorough naturalist, on completely familiar terms with current progress in these fields. His immediate successors also were. Some of us today are not. Much of the confusion in our terminology (for which we get such harsh criticism from fellow-scientists) reflects indiscriminate and ill-advised borrowings from neighboring sciences. The time has surely come for redefinition of our purposes and of the scope of our work. This book affords an historical perspective which can greatly help us.

It will be permitted to question the choice of the title. One would wish that Professor Conard had actually himself written a book which more truly outlined "the background of plant ecology." He is one of the few people who could write it. The present volume, however, is a translation of "Das Pflanzenleben der Donauländer." Nowhere is the original German title quoted.

Most of the text consists in description of landscape, and within landscape of zonations and distributions of communities. These are described both in terms of structure and floristic composition. Much detail is given as to soil and other physical factors that control communities. In fact all the elements of an accurate description of community are explicitly involved in Kerner's thinking: a) he does not fail—as many do today—to distinguish between flora and vegetation (see p. 4); b) he enu-

[1] **Conard, Henry S.** 1951. The background of plant ecology. A translation from the German of "The plant life of the Danube basin" by Anton Kerner (1863). x + 238 pp. Iowa State College Press, Ames, Iowa.

merates the elements of structure (the "life-forms" of a later day) and their assemblage into physiognomic units (pp. 4–9); c) he considers the development and replacement in time (p. 10).

In fact the idea of plant succession (and we mean community succession) is the object of an entire chapter (pp. 196–205). It is evident throughout the book that vegetation dynamics are a constant and conscious thought, not merely a vague apperception. Enough is said of the causes of succession to define it as a well-established mechanism; enough examples are given in different environments to substantiate Kerner's thinking on the subject.

The great service rendered by this translation, then, is to provide a very readable (if somewhat rhetorical) description of Central European vegetation and to make accessible, in their early form, some of the ideas that have since dominated many phases of plant ecology. Professor Conard has all too modestly remained in the background himself, whereas we should have had much interest in his own comments on many points raised by Kerner. Vierhapper, who issued the 2nd edition, added many marginal observations to Kerner's text and footnotes. (The latter, included in an appendix in the original, are not translated.) Of course the readers interested in details of identification and the finer points of history and interpretation can always consult the original. It is regrettable, however, that the excellent illustrations could not have been reproduced.

It is to be hoped that this book will reach a wide audience for it has appeal for the uninitiated as well as for those acquainted with current progress.

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Bird Populations of Georgia [1]

The material for this little book was presented as a master's thesis at the University of Georgia. The area covered is eight counties on the Dougherty Plains section of the Upper Coastal Plain, lying largely between the Flint and Chattahoochee rivers. The study was carried on from mid-June to late August in 1947 and 1948. Thirteen types of vegetation are recognized, and bird censuses were taken on a 70-acre plot of old fields and fence rows, a 43-acre tract of mature, dry longleaf pineland, and a 12.8-acre plot within a beech-magnolia hammock forest. More than three hundred birds were collected from the area as a whole.

An annotated list shows that 96 species summered in the region, distributed between 39 families and 16 orders. The families best represented were the Ardeidae (herons), Parulidae (warblers), Fringillidae (finches, grosbeaks, sparrows), and Picidae (woodpeckers).

Evidence is presented to show the northern affinities of many species and subspecies and it is suggested that this southward invasion of birds is correlated with the extension into the area of a Piedmont-type topography and vegetation. The reviewer is somewhat uncertain as to the significance of river valleys as southward invasion routes. He has noticed in the north that the first appearance of southern species is also most frequently in the river valleys. Could this be due to more continuous and undisturbed vegetation along the rivers than in the cultivated upland country?

The censuses indicated 66 pairs per 100 acres in old fields and fence rows, 197 pairs per 100 acres in pineland, and a surprising total of 740 pairs per 100 acres in the hammock forest. One is hesitant about accepting this last value as representing the true level of breeding populations in this type of vegetation because it is one of the highest on record, the five censuses came late in the breeding season (June 18 to August 10), the area was small, and several species listed are known ordinarily to have large territories. The reviewer suspects that a larger fraction of many territories extended outside of the actual sample plot than was allowed for and that perhaps there was an aggregation of birds in the area that were not actually nesting there.

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[1] **Norris, Robert A.** 1951. Distribution and populations of summer birds in southwestern Georgia. 67 pp., 1 drawing, 15 figs., maps, photographs; 6 tables; bibliography. Athens: Univ. Georgia Press. $1.25.

Studies in Late Tertiary Paleobotany [1]

The western United States is particularly rich in Tertiary floras. Comparison of these floras with their nearest modern equivalents enables paleobotanists to determine their systematic affinities, phytogeographical relationships, and ecological characteristics. The six papers included in the present volume represent important additions to the known fossil floras of the West and constitute valuable contributions toward the "reconstruction of Tertiary environment", particularly that of desert vegetation. These Late Tertiary floras approach closely their modern equivalents, as is readily evident from the plates, often showing "modern equivalent vegetation," as well as from the technical accounts of the species emphasizing the great similarity, if not actual identity, of the fossil leaves with those of modern species, and from the lists of fossil species accompanied by the names of similar living species. On the strength of this great morphological similarity, far-reaching conclusions are drawn regarding the ecological requirements and characteristics of the fossil species representing different floral elements and their components. A *Systematic Revision of Fossil Plants* is given as an appendix and a good index concludes the book.

The first paper (pp. 1–22), *Classification of the Madro-Tertiary Flora,* opens with theoretical discussions of the composition and classification of the major Tertiary floras. As the Madro-Tertiary flora, like other major Tertiary floras, includes vegetation types such as desert, woodland, arid subtropical scrub, sage, and chaparral, known to "occur on other continents as well", the author feels that each of these elements belongs to a higher category, for which he proposes the term *complex.* "A complex may be defined as a group of fossil species whose nearest modern equivalents now make up a distinctive vegetation type or plant formation that occurs on more than one continent." Analysis of the Madro-Tertiary Flora, for example, shows that in California it consists of 5 complexes, 8 elements, and 25 components (see Table 1, page 9).

A Sonoma Florule from Napa, California pp. 23–71, 4 pls.), consisting of 24 species, was found 35 mi. southeast of the three localities near Santa Rosa from where previously 44 species mainly of Arcto-Tertiary affinity had been reported. All of these floras from the San Francisco Bay region belong to "the most complete succession of late Tertiary floras now known in North America." The seven floras included in this clisere range "in age from transitional Mio-Pliocene to late Upper Pliocene." The age of the Napa florule was determined as Upper Pliocene, mainly on the strength of "local cliseral succession," as 91 per cent of its species occur in Miocene floras and 95 per cent in Pliocene floras.

Further Studies of the Mount Eden Flora, Southern California (pp. 73–117, 3 pls.) deal with new collections from the Mount Eden formation, the exact age of the flora, its composition and ecology. The total number of species now known is 47, the 17 newly recorded species all being woody. Arid subtropical scrub, desert-border, grassland, coastal sage, chaparral, live oak and walnut woodland, digger pine woodland, and big-cone forest are the plant communities represented in this flora. The age of this flora is Middle Pliocene, when a more humid and milder climate prevailed there than at present.

The discovery of *The Anaverde Flora of Southern California* (pp. 119–158, 3 pls.) of Middle Pliocene age furnished an important link in "the history of the modern desert flora and its contiguous vegetations." The 21 species reported in this paper are referred to live oak woodland, conifer woodland, chaparral, coastal sage, grassland, desert-border, and subtropical scrub communities.

The Piru Gorge Flora of Southern California (pp. 159–214, 6 pls.) "gives us our first information on the vegetation and climate of Ridge Basin," notable for its sediments recording "essentially continuous deposition from the end of Miocene into Upper Pliocene time." The 23 species of this flora were Middle Pliocene "members of woodland, chaparral, and border-forest vegetation", most of whose modern equivalents are still growing nearby in a climate that has remained essentially the same.

The last contribution (pp. 215–306, 3 pls., 4 figs.), *Evolution of Desert Vegetation in Western North America,* is likely to be of greatest interest to ecologists. Contrary to previously expressed views of the great age of deserts, the author attempts to prove that present desert environments of subcontinental extent "must be of latest Cenozoic age." Similarly desert floras elsewhere in the world developed in late Cenozoic time following more mesic types of vegetation during Cretaceous and early Tertiary periods. Deserts are regarded as "climatic accidents," as they were apparently "rare in earth history." These and other important conclusions are based on the analysis of approximately 110 fossil floras found within and around present desert regions of the Southwest and West, and

[1] **Axelrod, Daniel I.** 1950. Studies in late Tertiary paleobotany. 323 pp., 19 pls., 4 figs. Contributions to Paleontology. Carnegie Institution of Washington Publication **590**. Washington, D. C. Paperbound. $2.75.

comparison of the results with those based on other desert regions. Rather than invoke large-scale migrations of floras, the author believes "that the modern desert floras were derived largely from species which contributed to the more mesic Tertiary Floras that formerly extended across the present desert areas." "In other words, the modern desert species appear to be hardy plants derived from members of Tertiary communities that earlier dominated the region." Figure 4 (p. 287) illustrates these views diagrammatically by showing the floral succession and the relative extent of the important vegetation types for each of the three major desert regions (Northern Great Basin, Central Great Basin, Mohavia) during Middle and Upper Cenozoic times. Two major Tertiary Floras gave rise to most of the species of modern desert floras in the United States, namely the northern Arcto-Tertiary Flora and the more southern Madro-Tertiary Flora. Although placing the origin of modern deserts near the end rather than the beginning of the Tertiary, Axelrod reaffirms the accepted view of their geological and climatological origin and disproves unknowingly van Steenis' hypothesis (1936) of the anthropogenous origin of deserts.

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FOSSIL TAXODIACEAE IN WESTERN NORTH AMERICA [1]

Few botanical discoveries received the popular acclaim afforded the "discovery" of the living dawn redwood. Discovered in 1944 in China, this tree was successfully identified by two Chinese botanists with the genus Metasequoia, proposed in 1941 for Pliocene fossils from Japan. Professor Chaney promptly visited the remote part of China where Metasequoia is still growing, and thus obtained first-hand information regarding this tree, its habitat, and associates. His critical examination of thousands of American fossil specimens disclosed that many of them, especially those of Upper Cretaceous to Miocene age, belong to Metasequoia rather than to Sequoia and Taxodium. The series of errors and misidentifications, started about 100 years ago and continued by early and living paleobotanists, is fully exposed by the author. This story easily rivals that of the "discovery" in human interest.

Although younger strata of the American record lack Metasequoia, the genus was apparently common in older strata and widely distributed at that time. The American fossil material is referred to the five species recognized by the author under the three genera, Metasequoia (2), Sequoia (2), and Taxodium (1). The fossil equivalent of the living species, *M. glyptostroboides*, now bears Newberry's old name in a new combination, *M. occidentalis*. The phytogeographic and ecological importance of this find was treated by the author in an earlier paper (Proc. Nat. Acad. Sci. **34**: 503–515, 1948).

[1] **Chaney, Ralph W.** 1951. A revision of fossil Sequoia and Taxodium in western North America based on the recent discovery of Metasequoia. Transactions of the American Philosophical Society, new series, **40**, part 3 (1950): 171–263, 12 pls. Philadelphia, Pa. $1.50.

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"ARIZONA! MAGIC IS THY MELODIOUS NAME!" [1]

There has developed in this country a tradition that every state should have a book devoted to its birds, although its avifauna may not differ appreciably from that of the neighboring states, and the resulting book is little more than a repetition of previous knowledge, bolstered with very local distributional records, and embellished with costly color plates. The wisdom of this preoccupation with local records, and the vast expenditures of effort and money on lavish "state books" have often been questioned by those who feel that there are more valuable facets of ornithology—facets which can be as interesting to the amateur bird-watcher as they are to the professional ornithologist.

The one remaining state that might conceivably warrant a book of a general nature about its birds is Arizona, for within its borders are several species not found elsewhere in the United States, as well as a number of interesting endemic races. Brandt's "Arizona and its bird life" could have been a useful addition to the array of state books, but it is not. It is merely an expensive collection of colorful plates, anthropomorphic observations on birds, and prolix florid descriptions of Arizona.

[1] **Brandt, Herbert.** 1951. Arizona and its bird life, xvi + 724 pp., 21 color plates, numerous photographs and pen sketches. Cleveland, Ohio: The Bird Research Foundation. $15.00.

The choice of the title is unfortunate since it implies that the book is about all of the birds of Arizona, whereas it is only about some of the birds in less than one-tenth of the state. It is more adequately described in the lengthy subtitle, "A naturalist's adventures with the nesting birds on the deserts, grasslands, foothills and mountains of southeastern Arizona."

When first leafing through the pages of this huge book, one has the impression that it is merely a verbose narrative of the birding experiences of a man who is particularly proud of his "life list," and who was nearly overwhelmed by the splendor of Arizona. However, after reading the introduction and various sections in the body of the book, it is discovered that the author has attempted to create a technical treatise on the breeding birds of a diverse and highly interesting area. He has been thoroughly impressed by the need for the "scientific method" in ornithology and constantly calls the reader's attention, with pride, to his methods of collecting data, even allowing one a glimpse of a page from his field notes (p. 640). Nevertheless, the book is in no sense "scientific," although one cannot doubt the sincere intentions of the author.

If one has the patience to struggle through the tremendous mass of words, which the reviewer is under moral obligation to do, he will find the text studded with anthropomorphisms, exaggerations, and inaccuracies. For example, the cowbird which is childless and lax in its morals (pp. 160–161); the entire chapter (Chap. 42) which is devoted to an account of the discovery of a new race of wren (*Troglodytes brunneicollis vorhiesi*), which, in spite of being the first record of this species north of Mexico, hardly warrants the sensationalism which the author has given it; and the fact that the egg of a turkey is precocial (p. 636). There is only a very occasional reference in the text to the published literature and no list of what little has been cited, although the author must be familiar with the many publications on the avifauna of Arizona, since he says (p. xiv), that he has spent every free hour over a period of several years in research.

The book is not without some merits, however. It is beautifully printed and bound, and there is a splended collection of color plates, line drawings, and photographs by well-known artists and photographers. If one is willing to search through the book, he will find frequent references to the fact that the breeding season of many species may be delayed by prolonged dry seasons. Also, there are suggestions that the clutch-sizes of some species rise during, or even prior to, unusually wet periods, although the author is apparently unaware of the current interest and publications on these matters. One finds a useful annotated list of the breeding birds of the area studied (Sec. 6), and a long discussion of the avian populations in the various life zones of the region (Chap. 3). A description of a new race of martin (*Progne subis oberholseri*) is presented (p. 669), although such a book seems an inappropriate place for a taxonomic description.

The work will be of interest to those who collect beautiful bird books, but it hardly does justice to the avifauna of the state of which the author exclaims (p. 1) "Arizona! Magic is thy melodious name!"

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Studies of Gulls and Penguins

Few comprehensive long-term studies have been made of the breeding biology of colonial birds, owing to the usual inaccessibility of large avian populations and to the difficulties encountered when dealing with vast numbers of highly mobile animals. Within the past year two excellent publications concerned with avian aggregations have appeared, which are notable not only because they have resulted from years of careful observations, but also because of their fundamental ecological significance. Undoubtedly they will serve as touch-stones for future population work.

The first of these publications is a five-year study made by Paludan[1] of a colony of 1,200 pairs of herring gulls (*Larus argentatus*) and a colony of 1,000 pairs of lesser black-backed gulls (*Larus fuscus*), nesting on a group of islands in the Baltic. Most of the paper is concerned with a very useful account of the breeding behavior of the two species, which often differs markedly, but of even greater interest is the discussion of the population dynamics of the herring gull.

It was found that the clutch-size of the herring gull was almost invariably three eggs, although this could be reduced by the addition of foreign eggs to the nest shortly before egg laying began. Egg mortality was highly variable, but in a year in which there were no floods approximately ten per cent of the eggs failed to hatch. Chick mortality was heaviest during the first eight days after hatching, when seventy per cent of the young died. As the birds became older it

[1] **Paludan, Knud.** 1951. Contributions to the breeding biology of *Larus argentaus* and *Larus fuscus*. Vidensk. Medd. fra. Dansk naturh. Foren., **114**: 1–128.

was increasingly difficult to find them and to note their deaths, but it was estimated that not more than twenty per cent lived to leave the colony, or, in other words, less than one chick for each two pairs of adults.

A life table was constructed using nearly 1,000 recoveries of gulls banded as fledglings in Denmark from 1917 to 1942. Only birds recovered after August 30 of the year in which they were banded were included in the study in order to confine the life table to fully fledged birds. However, the rate of recovery for the first-year birds is probably disproportionately high because newly-fledged birds remain near the colony and are more easily recovered than the older, wide-ranging gulls.

Before it was possible to employ the life table data to ascertain whether sufficient young were being produced to maintain the population, it was necessary to establish the age at which the gulls begin to breed. Heretofore the herring gull has usually been thought to breed in its fourth year, since it is known that fully adult plumage is acquired in the fourth year and birds in immature plumage are rarely seen in a colony. Paludan found a breeding third-year gull in sub-adult plumage and from this slim evidence concluded that most of the birds breed in their third year, but that the banded individual was retarded in attaining its adult plumage. A more reasonable interpretation would appear to be that this was a bird breeding unusually early.

The life table indicates that there is 62 per cent mortality in the first year of adult life and that the rate then drops to roughly 15 per cent annually. Paludan points out that if 150 of every 1,000 sexually mature birds die annually, they must be replaced by 150 gulls which are breeding for the first time, if the population is to remain constant. It is difficult to estimate how many young must fledge in order to yield 150 adults two and one half years later, when, according to Paludan, they begin to breed, since the first year mortality rate as calculated in the life table is probably too high. However, using these figures, it was found that approximately 600 birds must be fledged. This is slightly more than one chick per pair of adults and twice the estimated production of the colony. Yet, in Denmark, as in North America, the population is known to be increasing. If the gulls do not breed until their fourth year the discrepancy is even greater.

Paludan then analyzed the earlier herring gull life tables of Marshall (Auk, **64**: 188–198, 1947) and of Paynter (Bird-Banding, **18**: 156–170, 1947) and found that the annual rate of mortality for sexually mature birds in North America is 29 per cent as opposed to 15 per cent in Denmark. Because the oldest record available for the North American life table compiled by Marshall is only 17 years, while there were five recoveries in the 26-year group in the Danish material, Paludan thought that the lower annual mortality rate for his birds may have been brought about by the longer span of the Danish study. To test for this, all of the Danish recoveries older than 17 years were discarded and the annual survival data were plotted on a semi-log graph and compared with the North American curve. The Danish mortality rate was raised somewhat but it was still considerably lower than the North American rate. It was then concluded that the difference is real, although the cause of the variation is unknown.

There is possibly one serious objection to this conclusion. In spite of the elaborate corrections which were necessary before Marshall's rather inadequate life table could be used, Paludan neglected the fact that although the North American table was constructed from returns from a 25-year period, very few gulls were banded in the early part of the period. In fact, Marshall included recoveries for only the years prior to 1940 and stated (*op. cit.*, p. 190), ". . . few Herring Gulls were banded in this country before 1921, ..." Therefore, recoveries of gulls even 17 years of age were very unlikely, simply because so few had been banded for so long. The importance of older birds in reducing the mean annual mortality rate may be very important, as has been shown by Paynter (Ecology, **30**: 146–166, 1949) in a later life table covering returns for 11 years, which, unfortunately, apparently was not seen by Paludan. In this paper it was shown that if one per cent of the birds live 25 years the mortality rate would drop to 14.5 per cent. It is interesting to note that approximately 0.5 per cent of Paludan's birds lived to their twenty-sixth year and the mean annual mortality was 15 per cent, which seems to confirm the earlier speculations of Paynter.

It appears, therefore, that eventually the life tables for the Danish and the North American gulls will be found to be similar. The fact that the Danish colony does not seem to be producing sufficient young to maintain the population may not be at all serious. In the Kent Island colony in New Brunswick Paynter found that only 50 per cent of the young are fledged. The 80 per cent loss estimated by Paludan may be found to be considerably lower if better techniques for locating the young can be devised. Also, it is possible that the mortality rate for the young chicks was abnormally high in the year in which the study was made.

The second of these outstanding publications on avian populations is the product of a ten-year study by Richdale of the sexual behavior of the yellow-eyed penguin (*Megadytes anti-*

podes) on the Otago Peninsula in New Zealand.[2]

The scope of the book is broader than the title would imply, since the term "sexual behavior" has been broadly interpreted to include information on measurements, weights, and molts, but only when they have some bearing on the general sexual behavior of the species. There are frequent discussions of similar patterns of behavior in other penguins as well as in other birds. These increase the breadth of the work and make it more useful to the reader who may be interested in the more general aspects of avian sexual behavior, rather than specifically in penguin behavior. There is an unfortunate paucity of references to European literature, but the difficulties in securing these publications in New Zealand are great and the author can hardly be blamed for his unfamiliarity with them.

A unique feature of the study, aside from the many years it required, is the author's intimate knowledge of each bird. This was achieved by banding every individual with especially made bands which could be read with the aid of a telescope at considerable distances. The idiosyncrasies of each of the 88 males and 96 females, in nearly 300 matings, are thereby fully known.

The body of the book consists of ten chapters which in turn deal with the scope of the study, an analysis of the types of behavior, pair formation, sexual dimorphism, sexual behavior in the winter, the pre-egg stage, unemployed birds, incubation, the chick stage, and molting. At the end of each chapter there is a very useful summary. The appendices are concerned with accounts of the behavior of individual birds, which are too detailed to be of general interest, but offer an insight into the thorough nature of the study and the material from which the general conclusions were drawn. The plates are an integral part of the work and illustrate, often strikingly, many of the postures discussed in the text. It is unfortunate that unskillful retouching has marred a number of them.

Anthropomorphism has been scrupulously avoided, although in glancing through the pages the reader will note frequent references to "sheepish looks," "glares," "divorce," etc. These have been used to describe particular actions and do not bear the strict connotations associated with human behavior. The choice of these terms appears unfortunate at times, but as they are defined rigorously and used consistently they do not detract from the work if one first reads the definitions presented by the author.

In a short review it is impossible to do justice to the wealth of entirely new information found in this book. Without doubt it is one of the classic ornithological studies of the century and should maintain its high position for many years.

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[2] **Richdale, L. E.** 1951. Sexual behavior in penguins. xiv + 316 pp., 22 figs. Lawrence, Kansas: University of Kansas Press. $5.00.

INSTINCTIVE BEHAVIOR [1]

This book is an extension of a series of lectures delivered by the author in 1947 under the auspices of the American Museum of Natural History and Columbia University. His avowed aim in publishing this material is two-fold; to acquaint Anglo-American readers with European research in ethology, and to attempt to frame a formally consistent approach to problems of patterned behavior.

Delay in publication has made some of the examples cited familiar to English readers through the medium of a recent symposium on animal behavior published by the Society for Experimental Biology. However, much of the material presented is not readily available elsewhere and the framework of Tinbergen's argument justifies what repetition there is. An attempt to cover such a broad field in such short compass is necessarily condensed. Fortunately the author presents his material lucidly and does not descend to the succinct vagueness of review articles.

The first half of the book is a discussion of the characteristics of instinctive behavior and its endogenous and exogenous causal factors. This discussion leads to a tentative definition of an instinct "as a hierarchically organized nervous mechanism which is susceptible to certain priming, releasing and directing impulses of internal as well as external origin, and which responds to these impulses by coordinated movements that contribute to the maintenance of the individual and the species." Each element in this definition is discussed, particular stress being laid on the hierarchical character of instinctive behavior. This aspect of behavior leads Tinbergen to postulate a group of nervous centers responsible for the activation of a motor re-

[1] **Tinbergen, Nicholas.** 1951. The study of instinct. xii + 228 pp. Oxford: Clarendon Press. 25 s.

sponse when "released" by an appropriate stimulus. This release also permits potential activation of a lower-order center on presentation of its appropriate stimulus and so on until the sequence is terminated in the release of the consummatory act. This permits resolution of the nagging question of the plasticity or rigidity of instinctive behavior, since the motor set controlled by each center is termed an instinctive act. Descent of the hierarchy is characterized by increasing rigidity while the highest levels exhibit great plasticity.

This formulation of the hierarchical character of instinctive behavior permits the author to establish connections with neurophysiology at two points. He points out that Weiss's concept of hierarchy in central nervous system organization is coterminal with the formulation outlined above. Secondly he cites the work of Hess who succeeded in producing complete patterns of fighting, eating, and sleep by artificial local stimulation of the hypothalamus of intact animals.

The remainder of the book consists of essays on the ontogeny, phylogeny and adaptiveness of instinctive behavior.

A third aim, patent throughout the book, is a careful definition of minimum standards in ethological work. The complexity of the phenomena studied makes workers in this area painfully susceptible to the pitfalls of oversimplification. In standardization of conditions, both internal and external factors must be considered. Further, results become meaningful only in the context of the totality of the patterned hierarchy. Throughout, the author's discussion of such considerations is lucid and compelling.

This is a preliminary formulation of fragmentary data clothed at points by a monolayer of fact. Its tentative and exploratory character is made explicit by the author in his preface. It is at the same time a formulation of power ample to compel careful and critical marshalling of evidence by both proponents and dissenters. It is further a formulation which is sufficiently precise to guide subsequent research. It is, finally, thoroughly enjoyable and fascinating reading.

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BOOK NOTICE

Berner, Lewis. 1950. *The mayflies of Florida.* University of Florida Studies, Biological Science Series, **4** (4). xii + 267 pp., 24 plates, 88 text figs., 19 maps. Gainesville: Univ. of Florida Press. $5.50 (paper bound).

Florida has a small mayfly fauna, Dr. Berner and his colleagues having discovered only 48 species during intensive collecting in most parts of the State. Florida lacks the swift, rocky, streams characteristic of regions where Ephemeroptera are most abundant in numbers of species as well as individuals. However, the mayflies have in the past been very inadequately investigated. as is emphasized by the fact that 42 of the 48 species were first recorded for Florida by Dr. Berner, and of these 42, about 20 were new to science.

In this handsomely printed and handsomely priced volume there is a general discussion of mayfly biology and taxonomy, followed by a very fully annotated list of the Florida species. The general section includes Berner's views on comparative ecology and zoogeography of mayflies. He suggests that the endemic Florida species may all have evolved from northerly stocks since the establishment of Florida as a peninsula in the Pleistocene. He notes that not one West Indian species is known from Florida. One interesting generalization is that all of the species found both in the North and in Florida show no seasonality of emergence and mating in the South but have "a rather limited period of emergence during late spring and summer" in the North.

Preceding the "Annotated List" are keys to the adults of 46 species and subspecies and the nymphs of 48 species and subspecies. The annotations are composed of very detailed notes on life-history and habits, brief taxonomic remarks, and complete locality records for each species. The known range is summarized on distribution maps. Beautiful half-tone plates, each showing the entire insect, illustrate the male imagines of 7 species and the nymphs of 17. These are esthetically pleasing but perhaps are not the ideal illustrations to aid in making determinations.

Limnologists working in the Southeast should find this a valuable reference book. *Charles L. Remington.*

ANNOUNCEMENT

University of Texas Institute of Marine Science

Facilities for studies in marine biology are now available at the Institute of Marine Science of the University of Texas. Course-work and problems for qualified graduates are offered in ecology and fisheries biology under M. D. Burkenroad and G. Gunter. Living quarters and a research vessel are available. The dock-laboratory on Aransas Pass provides unique opportunities for a variety of investigations. Enquiries should be addressed to the Acting Director, Port Aransas, Texas.